HAND-BOOK

OF

PHYSIOLOGY.

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PREFACE TO THE EIGHTH EDITION.

The Eighth Edition is the result of an increased demand for this work, involving the necessity for a reprint at an earlier period after the publication of the Seventh Edition than was anticipated. The opportunity has been seized for making corrections and additions where they appeared to be most needed; but the present issue must be regarded as, in great part, a reprint of the Edition of 1869.

W. MORRANT BAKER.

The College, St. Bartholomew's Hospital,
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Page 150, 4th line from bottom, the words "as in Fig. 46" to be transferred to the end of the 13th line from top of p. 151.

Page 175, 12th line from bottom, *for* "secret" *read* "recent."

HANDBOOK OF PHYSIOLOGY.

CHAPTER I.

ON THE GENERAL AND DISTINCTIVE CHARACTERS OF LIVING BEINGS.

HUMAN PHYSIOLOGY is the science which treats of the life of man—of the way in which he lives, and moves, and has his being. It teaches how man is begotten and born; how he attains maturity; and how he dies.

Having, then, man as the object of its study, it is unnecessary to speak here of the laws of life in general, and the means by which they are carried out, further than is requisite for the more clear understanding of those of the life of man in particular. Yet it would be impossible to understand rightly the working of a complex machine without some knowledge of its motive power in the simplest form; and it may be well to see first what are the so-called essentials of life—those, namely, which are manifested by all living beings alike, by the lowest vegetable and the highest animal, before proceeding to the consideration of the structure and endowments of the organs and tissues belonging to man.

The essentials of life are these,—birth, growth and development, decline and death—and an idea of what life is, will be best gained by sketching these events, each in succession, and their relations one to another.

The term, birth, when employed in this general sense of one of the conditions essential to life, without reference to

any particular kind of living being, may be taken to mean, separation from a parent, with a greater or less power of independent existence as a living being.

Taken thus, the term, although not defining any particular stage in development, serves well enough for the expression of the fact, to which no exception has yet been proved to exist, that the capacity for life in all living beings is got by inheritance.

Growth, or inherent power of increasing in size, although essential to our idea of life, is not a property of living beings only. A crystal of sugar or of common salt, or of any other substance, if placed under appropriate conditions for obtaining fresh material, will grow in a fashion as definitely characteristic and as easily to be foretold as that of a living creature. It is, therefore, necessary to explain the distinctions which exist in this respect between living and lifeless structures; for the manner of growth in the two cases is widely different.

First, the growth of a crystal, to use the same example as before, takes place merely by additions to its outside; the new matter is laid on particle by particle, and layer by layer, and, when once laid on, it remains unchanged. The growth is here said to be *superficial*. In a living structure, on the other hand, as, for example, a brain or a muscle, where growth occurs, it is by addition of new matter, not to the surface only, but throughout every part of the mass; the growth is not superficial, but *interstitial*. In the second place, all living structures are subject to constant decay; and life consists, not as once supposed, in the power of preventing this never-ceasing decay, but rather in making up for the loss attendant on it by never-ceasing repair. Thus, a man's body is not composed of exactly the same particles day after day, although to all intents he remains the same individual. Almost every part is changed by degrees; but the change is so gradual, and the renewal of that which is lost so exact, that no difference may be noticed, except at

long intervals of time. A lifeless structure, as a crystal, is subject to no such laws; neither decay nor repair is a necessary condition of its existence. That which is true of structures which never had to do with life is true also with respect to those which, though they are formed by living parts, are not themselves alive. Thus, an oyster shell is formed by the living animal which it encloses, but it is as lifeless as any other mass of saline matter; and in accordance with this circumstance its growth takes place not *interstitially*, but layer by layer, and it is not subject to the constant decay and reconstruction which belong to the living. The hair and nails are examples of the same fact.

Thirdly,—in connection with the growth of lifeless masses there is no alteration in composition or properties of the material which is taken up and added to the previously existing mass. For example, when a crystal of common salt grows on being placed in a fluid which contains the same material, the properties of the salt are not changed by being taken out of the liquid by the crystal and added to its surface in a solid form. But the case is essentially different from this in living beings, both animal and vegetable. A plant, like a crystal, can only grow when fresh material is presented to it; and this is absorbed by its leaves and roots; and animals for the same purpose of getting new matter for growth and nutrition, take food into their stomachs. But in both these cases the materials are much altered before they are finally *assimilated* by the structures they are destined to nourish.

Fourthly. The growth of all living things has a definite limit, and the law which governs this limitation of increase in size is so invariable that we should be as much astonished to find an individual plant or animal without limit as to growth as without limit to life.

Development is as constant an accompaniment of life as growth. The term is used to indicate that change to

which, before maturity, all living parts are constantly subject, and by which they are made more and more capable of performing their several functions. For example, a full-grown man is not simply a magnified child; his tissues and organs have not only grown, or increased in size, they have also *developed*, or become better in quality.

No very accurate limit can be drawn between the end of development and the beginning of decline; and the two processes may be often seen together in the same individual. But after a time all parts alike share in the tendency to degeneration, and this is at length succeeded by death.

The decline of living beings is as definite in its occurrence as growth or development. Death—not by disease or injury—so far from being a violent interruption of the course of life, is but the fulfilment of a purpose in view from the commencement.

It has been already said that the essential features of life are the same in all living things; in other words, in the members of both the animal and vegetable kingdoms. It may be well now to notice briefly the distinctions which exist beween the members of these two kingdoms. It may seem, indeed, a strange notion that it is possible to confound vegetables with animals, but it is true with respect to the lowest of them, in which but little is manifested beyond the essentials of life, which are the same in both.

I. Perhaps the most essential distinction is the presence or absence of power to live upon *inorganic* material; in other words, to act chemically on carbonic acid, ammonia and water, so as to make use of their component elements as food. Indeed one ought probably to say that a question concerning the capability of the lower kinds of animal to live in this way cannot be entertained; and that such a manner of life should decide at once in favour of a vegetable nature, whatever might be the attributes which *seemed to* point to an opposite conclusion. The power of

living upon *organic* matter would seem to be less decisive of an animal nature, for some fungi appear to derive support almost entirely from this source.

II. There is, commonly, a marked difference in general chemical composition between vegetables and animals, even in their lowest forms; for while the former consist mainly of a substance containing carbon, hydrogen, and oxygen only, arranged so as to form a compound closely allied to starch, and called cellulose, the latter are commonly composed in great part of the three elements just named, together with a fourth, nitrogen; the proximate principles formed from these being identical, or nearly so, with albumen. It must not be supposed, however, that either of these typical compounds alone, with its allies, is confined to one kingdom of nature. Nitrogenous or albuminous compounds are freely produced by vegetable structures, although they form an infinitely smaller proportion of the whole organism than cellulose or starch. And while the presence of the latter in animals is much more rare than is that of the former in vegetables, there are many animals in which traces of it may be discovered, and some, the Ascidians, in which it is found in considerable quantity.

III. Inherent power of movement is a quality which we so commonly consider an essential indication of animal nature, that it is difficult at first to conceive it existing in any other. The capability of simple motion is now known, however, to exist in so many vegetable forms, that it can no longer be held as an essential distinction between them and animals, and ceases to be a mark by which the one can be distinguished from the other. Thus the zoospores of many of the Cryptogamia exhibit movements of a like kind to those seen in animalcules; and even among the higher orders of plants, many exhibit such motion, either at regular times, or on the application of external irritation, as might lead one, were this fact taken by itself, to

regard them as sentient beings. Inherent power of movement, then, although especially characteristic of animal nature, is, when taken by itself, no proof of it. Of course, if the movement were such as to indicate any kind of purpose, whether of getting food or any other, the case would be different, and we should justly call a being exhibiting such motion, an animal. But low down in the scale of life, where alone there exists any difficulty in distinguishing the two classes, movements, although almost always more lively, are scarcely or not at all more purposive in one than the other; and even if we decide on the animal nature of a being, it by no means follows that we are bound to acknowledge the presence of sensation or volition in the slightest degree. There may be at least no evidence of its possessing a trace of those tissues, nervous and muscular, by which, in the higher members of the animal kingdom, these qualities are manifested. Probably thère is no more of either of them in the lowest animals than in vegetables. In both, movement is effected by the same means—ciliary action, and hence the greater value, for purposes of classification, of the power to live on this or that kind of food,—on organic or inorganic matter. As the main purpose of the lowest members of the vegetable kingdom is doubtless to bring to organic shape the elements of the inorganic world around, so the function of the lowest animals is, in like manner, to act on degenerating organic matter,—"to arrest the fugitive organized particles, and turn them back into the ascending stream of animal life." And, because sensation and volition are accompaniments of life in somewhat higher animal forms, it is needless to suppose that these qualities exist under circumstances in which, as we may believe, they could be of no service. It is as needless as to dogmatise on the opposite side, and say that no feeling or voluntary movement is possible without the presence of those tissues which we call nervous and muscular.

IV. The presence of a stomach is a very general mark by which an animal can be distinguished from a vegetable. But the lowest animals are surrounded by material that they can take as food, as a plant is surrounded by an atmosphere that it can use in like manner. And every part of their body being adapted to absorb and digest, they have no need of a special receptacle for nutrient matter, and accordingly have no stomach. This distinction then is not a cardinal one.

It would be tedious as well as unnecessary to enumerate the chief distinctions between the more highly developed animals and vegetables. They are sufficiently apparent. It is necessary to compare, side by side, the lowest members of the two kingdoms, in order to understand rightly how faint are the boundaries between them.

CHAPTER II.

CHEMICAL COMPOSITION OF THE HUMAN BODY.

THE following *Elementary Substances* may be obtained by chemical analysis from the human body: Oxygen, Hydrogen, Nitrogen, Carbon, Sulphur, Phosphorus, Silicon, Chlorine, Fluorine, Potassium, Sodium, Calcium, Magnesium, Iron, and, probably as accidental constituents, Manganesium, Aluminium, Copper, and Lead. Thus, of the sixty-three or more elements of which all known matter is composed, more than one fourth are present in the human body.

Only one or two elements, and in very minute amount, are present in the body uncombined with others; and even these are present much more abundantly in various states of combination. The most simple compounds formed

by union in various proportions of these elements are termed *proximate* principles; while the latter are classified as the *organic* and the *inorganic* proximate principles.

The term *organic* was once applied exclusively to those substances which were thought to be beyond the compass of synthetical chemistry and to be formed only by *organized* or living beings, animal or vegetable; these being called organized, inasmuch as they are characterized by the possession of different parts called organs. But with advancing knowledge, both distinctions have disappeared; and while the title of living organism is applied to numbers of living things, having no trace of organs in the old sense of the term, and in some, so far as can be now seen, in no other sense, the term organic has long ceased to be applied to substances formed only by living tissues. In other words, substances, once thought to be formed only by living tissues, are still termed organic, although they can be now made in the laboratory. The term, indeed, in its old meaning, becomes year by year applicable to fewer substances, as the chemist adds to his conquests over inorganic elements and compounds, and moulds them to more complex forms.

Although a large number of so-called organic compounds have long ceased to be peculiar in being formed only by living tissues, the terms organic and inorganic are still commonly used to denote distinct classes of chemical substances, and the classification of the matters of which the human body is composed into the organic and the inorganic is convenient, and will be here employed.

No very accurate line of separation can be drawn between organic and inorganic substances, but there are certain peculiarities belonging to the former which may be here briefly noted.

1. Organic compounds are composed of a larger number of *Elements* than are present in the more common kinds of inorganic matter. Thus, albumen, fibrin, and gelatin, the

most abundant substances of this class, in the more highly organized tissues of animals, are composed of five elements, —carbon, hydrogen, oxygen, nitrogen, and sulphur. The most abundant inorganic substance, water, has but two elements, hydrogen and oxygen,

2. Not only are a large number of elements usually combined in an organic compound, but a large number of *equivalents* or *atoms* of each of the elements are united to form an equivalent or atom of the compound. In the case of carbonate of ammonium, as an example among inorganic substances, one equivalent of carbonic acid is united with two of ammonium; the equivalent or atom of carbonic acid consists of one of carbon with two of oxygen; and that of ammonium of one of nitrogen with three of hydrogen. But in an equivalent or atom of fibrin, or of albumen, there are of the same elements, respectively, 72, 22, 18, and 112 equivalents. And, together with this union of large numbers of equivalents in the organic compound, it is further observable, that the several numbers stand in no simple arithmetical relation one with another, as the numbers of equivalents combining in an inorganic compound do.

With these peculiarities in the chemical composition of organic bodies we may connect two other consequent facts; first, the large number of different compounds that are formed out of comparatively few elements; secondly, their great proneness to decomposition. For it is a general rule, that the greater the number of equivalents or atoms of an element that enter into the formation of an atom of a compound, the less is the stability of that compound. Thus, for example, among the various oxides of lead and other metals, the least stable in composition are those in which each equivalent has the largest number of equivalents of oxygen. So, water, composed of one equivalent of oxygen and two of hydrogen, is not changed by any slight force; but peroxide of hydrogen, which has two

equivalents of oxygen to two of hydrogen, is among the substances most easily decomposed.

The instability, on this ground, belonging to organic compounds, is, in those which are most abundant in the highly organized tissues of animals, augmented, 1st, by their containing nitrogen, which, among all the elements, may be called the least decided in its affinities, and that which maintains with least tenacity its combinations with other elements; and, 2ndly, by the quantity of water which, in their natural state, is combined with them, and the presence of which furnishes a most favourable condition for the decomposition of nitrogenous compounds. Such, indeed, is the instability of animal compounds, arising from these several peculiarities in their constitution, that, in dead and moist animal matter, no more is requisite for the occurrence of decomposition than the presence of atmospheric air and a moderate temperature; conditions so commonly present, that the decomposition of dead animal bodies appears to be, and is generally called, spontaneous. The modes of such decomposition vary according to the nature of the original compound, the temperature, the access of oxygen, the presence of microscopic organisms, and other circumstances, and constitute the several processes of decay and putrefaction; in the results of which processes the only general rule seems to be, that the several elements of the orginal compound finally unite to form those substances, whose composition is, under the circumstances, most stable.

The *organic* compounds existing in the human body may be arranged in two classes, namely, the *azotized*, or *nitrogenous*, and the *non-azotised*, or *non-nitrogenous* principles.

The *non-azotized* principles include the several fatty, oily, or oleaginous substances, as olein, stearin, cholesterin, and others. In the same category of non-nitrogenous substances may be included lactic and formic acids, animal glucose, sugar of milk, &c.

The oily or fatty matter which, enclosed in minute cells, forms the essential part of the adipose or fatty tissue of the human body (p. 38), and which is mingled in minute particles in many other tissues and fluids, consists of a mixture of *stearin*, *palmitin*, and *olein*. The mixture forms a clear yellow oil, of which different specimens congeal at from 45° to 35°.

Cholesterin, a fatty matter which melts at 293° F., and is therefore, always solid at the natural temperature of the body, may be obtained in small quantity from blood, bile, and nervous matter. It occurs abundantly in many biliary calculi; the pure white crystalline specimens of these concretions being formed of it almost exclusively. Minute rhomboidal scale-like crystals of it are also often found in morbid secretions, as in cysts, the puriform matter of softening and ulcerating tumours, &c. It is soluble in ether and boiling alcohol; but alkalies do not change it; it is one of those fatty substances which are not saponifiable.

The *azotized* or *nitrogenous* principles in the human body include what may be called the proper *gelatinous* and *albuminous* substances, besides others of less definite rank and composition, as pepsin and ptyalin, horny matter or keratin, many colouring and extractive matters, &c.

The *gelatinous* substances are contained in several of the tissues, especially those which serve a passive mechanical office in the economy; as the cellular, or fibro-cellular tissue in all parts of the body, the tendons, ligaments, and other fibrous tissues, the cartilages and bones, the skin and serous membranes. These, when boiled in water, yield a material, the solution of which remains liquid while it is hot, but becomes solid and jelly-like on cooling.

Two varieties of these substances are described, *gelatin* and *chondrin*, the latter being derived from cartilages, the former from all the other tissues enumerated above,

and in its purest state, from isinglass, which is the swimming bladder of the sturgeon, and which, with the exception of about 7 per cent. of its weight, is wholly reducible into gelatin. The most characteristic property of gelatin is that already mentioned, of its solution being liquid when warm, and solidifying or setting when it cools. The temperature at which it becomes solid, the proportion of gelatin which must be in solution, and the firmness of the jelly when formed, are various, according to the source, the quantity, and the quality of the gelatin; but, as a general rule, one part of dry gelatin dissolved in 100 of water, will become solid when cooled to 60°. The solidified jelly may be again made liquid by heating it, and the transitions from the solid to the liquid state by the alternate abstraction and addition of heat, may be repeated several times; but at length the gelatin is so far altered, and, apparently, oxydized by the process, that it no longer becomes solid on cooling. Gelatin in solutions too weak to solidify when cold, is distinguished by being precipitable with alcohol, ether, tannic acid, and bichloride of mercury, and not precipitable with the ferrocyanide of potassium. The most delicate and striking of these tests is the tannic acid, which is conveniently supplied in an infusion of oak-bark or gall-nuts; it will detect one part of gelatin in 5,000 of water; and if the solution of gelatin be strong it forms a singularly dense and heavy precipitate, which has been named tanno-gelatin, and is completely insoluble in water.

Chondrin, the kind of gelatin obtained from cartilages agrees with gelatin in most of its characters, but its solution solidifies on cooling much less firmly, and, unlike gelatin, it is precipitable with acetic and the mineral and other acids, and with alum, persulphate of iron and acetate of lead.

Albuminous substances, or *proteids*, as they are sometimes *called, exist* abundantly in the human body. The chief

among them are albumen, fibrin, casein, syntonin, myosin, and globulin.

Albumen exists in most of the tissues of the body, but especially in the nervous, in the lymph, chyle, and blood, and in many morbid fluids, as the serous secretions of dropsy, pus, and others. In the human body it is most abundant, and most nearly pure, in the serum of the blood. In all the forms in which it naturally occurs, it is combined with about six per cent. of fatty matter, phosphate of lime, chloride of sodium, and other saline substances. Its most characteristic property is, that both in solution and in the half-solid state in which it exists in white-of-egg, it is coagulated by heat, and in thus becoming solid, becomes insoluble in water. The temperature required for the coagulation of albumen is the higher the less the proportion of albumen in the solution submitted to heat. Serum and such strong solutions will begin to coagulate at from 150° to 170°, and these, when the heat is maintained, become almost solid and opaque. But weak solutions require a much higher temperature, even that of boiling, for their coagulation, and either only become milky or opaline, or produce flocculi which are precipitated.

Albumen, in the state in which it naturally occurs, appears to be but little soluble in pure water, but is soluble in water containing a small proportion of alkali. In such solutions it is probably combined chemically with the alkali; it is precipitated from them by alcohol, nitric, and other mineral acids, by ferrocyanide of potassium (if before or after adding it the alkali combined with the albumen be neutralised), by bichloride of mercury, acetate of lead, and most metallic salts.

Coagulated albumen, *i.e.*, albumen made solid with heat, is soluble in solutions of caustic alkali, and in acetic acid if it be long digested or boiled with it. With the aid of heat, also, strong hydrochloric acid dissolves albumen pre-

viously coagulated, and the solution has a beautiful purple or blue colour.

Fibrin is found most abundantly in the blood and the more perfect portions of the lymph and chyle. It is very doubtful, however, whether fibrin, as such, exists in these fluids,—whether, that is to say, it is not itself formed at the moment of coagulation. (See Chapter on the Blood).

If a common clot of blood be pressed in fine linen while a stream of water flows upon it, the whole of the blood-colour is gradually removed, and strings and various pieces remain of a soft, yet tough, elastic, and opaque-white substance, which consist of fibrin, impure, with a mixture of fatty matter, lymph-corpuscles, shreds of the membranes of red blood-corpuscles, and some saline substances. Fibrin somewhat purer than this may be obtained by stirring blood while it coagulates, and collecting the shreds that attach themselves to the instrument, or by retarding the coagulation, and, while the red blood-corpuscles sink, collecting the fibrin unmixed with them. But in neither of these cases is the fibrin perfectly pure.

Chemically, fibrin and albumen can scarcely be distinguished; the only difference apparently being that fibrin contains 1·5 more oxygen in every 100 parts than albumen does. Mr. A. H. Smee has, indeed, apparently converted albumen into fibrin, by exposing a solution to the prolonged influence of oxygen. Nearly all the changes, produced by various agents, in coagulated albumen, may be repeated with coagulated fibrin, with no greater differences of result than may be reasonably ascribed to the differences in the mechanical properties of the two substances. Of such differences, the principal are, that immersed in acetic acid swells up and becomes transparent like gelatin, while albumen undergoes no such apparent change; and that deutoxyde of hydrogen is decomposed when in compact with coagulated fibrin, but not with albumen.

Casein, which is said to be albumen in combination with

soda, exists largely in milk, and forms one of its most important constituents.

Syntonin is obtained from muscular tissue, both of the striated and organic kind. It differs from ordinary fibrin in several particulars, especially in being less soluble in nitrate and carbonate of potash, and more soluble in dilute hydrochloric acid.

Myosin is the substance which spontaneously coagulates in the juice of muscle. It is closely allied to syntonin; indeed, in the act of solution in dilute acids, it is converted into it.

The per-centage composition of albumen, fibrin, gelatin, and chondrin, is thus given by Mulder :—

	Albumen.	Fibrin.	Gelatin.	Chondrin.
Carbon	53·5	52·7	50·40	49·97
Hydrogen	7·0	6·9	6·64	6·63
Nitrogen	15·5	15.4	18·34	14·44
Oxygen	22·0	23·5	24·26	28·58
Sulphur	1.6	1·2		0·38
Phosphorus	0.4	0·3		
	100·0	100·0	100·00	100·00

Horny Matter.—The substance of the horny tissues, including the hair and nails (with whale-bone, hoofs, and horns), consists of an albuminous substance, with larger proportions of sulphur than albumen and fibrin contain. Hair contains 10 per cent. and nails 6 to 8 per cent. of sulphur.

The horny substances, to which Simon applied the name of *keratin*, are insoluble in water, alcohol, or ether; soluble in caustic alkalies, and sulphuric, nitric, and hydrochloric acids; and not precipitable from the solution in acids by ferrocyanide of potassium.

Mucus, in some of its forms, is related to these horny substances, consisting, in great part, of epithelium detached

from the surface of mucous membrane, and floating in a peculiar clear and viscid fluid. But under the name of mucus, several various substances are included of which some are morbid albuminous secretions containing mucus and pus-corpuscles, and others consist of the fluid secretion variously altered, concentrated, or diluted. Mucus contains an albuminous substance, termed *mucin*. It differs from albumen chiefly in not containing sulphur.

Pepsin and other albuminous *ferments*, as they are sometimes called, will be described in connection with the secretions of which they are the active principles. And the various *colouring matters*, as of the blood, bile, &c., will be also considered with the fluids or tissues to which they belong.

Besides the above-mentioned organic nitrogenous compounds, other substances are formed in the living body, chiefly by decomposition of nitrogenous materials of the food and of the tissues, which must be reckoned rather as temporary constituents than essential component parts of the body; although from the continual change, which is a necessary condition of life, they are always to be found in greater or less amount. Examples of these are urea, uric, and hippuric acid, creatin, creatinin, leucin, and many others.

Such are the chief organic substances of which the human body is composed. It must not be supposed, however, that they exist naturally in a state approaching that of chemical purity. All the fluids and tissues of the body appear to consist, chemically speaking, of mixtures of several of these principles, together with saline matters. Thus, for example, a piece of muscular flesh would yield fibrin, albumen, gelatin, fatty matters, salts of soda, potash, lime, magnesia, iron, and other substances, such as creatin, which appear passing from the organic towards the inorganic state. This mixture of substances may be explained in some measure by the existence of many

different structures or tissues in the muscles; the gelatin may be referred principally to the cellular tissue between the fibres, the fatty matter to the adipose tissue in the same position, and part of the albumen to the blood and the fluid by which the tissue is kept moist. But, beyond these general statements, little can be said of the mode in which the chemical compounds are united to form an organized structure; or of how, in any organic body, the several incidental substances are combined with those which are essential.

The *inorganic* matters which exist as such in the human body are numerous.

Water forms a large proportion, probably more than two-thirds of the weight of the whole body.

Phosphorus occurs in combination,—as in the neutral phosphate of sodium in the blood and saliva, the acid phosphates of the muscles and urine, the basic phosphates of calcium and magnesium in the bones and teeth.

Sulphur is present chiefly in the sulphocyanide of potassium of the saliva, and in the sulphates of the urine and sweat.

A very small quantity of *silica* exists, according to Berzelius, in the urine, and, according to others, in the blood. Traces of it have also been found in bones, in hair, and in some other parts of the body.

Chlorine is abundant in combination with sodium, potassium, and other bases in all parts, fluid as well as solid, of the body. A minute quantity of *fluorine* in combination with calcium has been found in the bones, teeth, and urine.

Potassium and *sodium* are constituents of the blood and all the fluids, in various quantities and proportions. They exist in the form of chlorides, sulphates, and phosphates, and probably, also, in combination with albumen, or certain organic acids. Liebig, in his work on the Chemistry of Food, has shown that the juice expressed from muscular

flesh always contains a much larger proportion of potash-salts than of soda-salts; while in the blood and other fluids, except the milk, the latter salts always preponderate over the former; so that, for example, for every 100 parts of soda-salts in the blood of the chicken, ox, and horse, there are only 40·8, 5·9, and 9·5 parts of potash-salts; but for every 100 parts of soda-salts in their muscles, there are 381, 279, and 285 parts of potash-salts.

The salts of *calcium* are by far the most abundant of the earthy salts found in the human body. They exist in the lymph, chyle, and blood, in combination with phosphoric acid, the phosphate of calcium being probably held in solution by the presence of phosphate of sodium. Perhaps no tissue is wholly void of phosphate of calcium; but its especial seats are the bones and teeth, in which, together with carbonate and fluoride of calcium, it is deposited in minute granules, in a peculiar compound, named bone-earth, containing 51·55 parts of lime, and 48·45 of phosphoric acid. Phosphate of calcium, probably the neutral phosphate, is also found in the saliva, milk, bile, and most other secretions, and acid phosphate in the urine, and, according to Blondlot, in the gastric fluid.

Magnesium appears to be always associated with calcium, but its proportion is much smaller, except in the juice expressed from muscles, in the ashes of which magnesia preponderates over lime.

The especial place of *iron* is in the hæmo-globin, the colouring-matter of the blood, of which a further account will be given with the chemistry of the blood. Peroxyde of iron is found, in very small quantities, in the ashes of bones, muscles, and many tissues, and in lymph and chyle, albumen of serum, fibrin, bile, and other fluids; and a salt of iron, probably a phosphate, exists in considerable quantity in the hair, black pigment, and other deeply coloured epithelial or horny substances.

Aluminium, Manganese, Copper, and *Lead*.—It seems most

likely that in the human body, *copper*, *manganesium*, *aluminium*, and *lead* are merely accidental elements, which, being taken in minute quantities with the food, and not excreted at once with the fæces, are absorbed and deposited in some tissue or organ, of which, however, they form no necessary part. In the same manner, *arsenic*, being absorbed, may be deposited in the liver and other parts.

CHAPTER III.

STRUCTURAL COMPOSITION OF THE HUMAN BODY.

In the investigation of the *structural* composition of the human body, it will be well to consider in the first place, what are the simplest anatomical elements which enter into its formation, and then proceed to examine those more complicated tissues which are produced by their union.

It may be premised, that in all the living parts of all living things, animal and vegetable, there is invariably to be discovered, entering into the formation of their anatomical elements, a greater or less amount of a substance, which, in chemical composition and general characters, is indistinguishable from albumen. As it exists in a living tissue or organ, it differs essentially from mere albumen in the fact of its possessing the power of growth, development, and the like; but in chemical composition it is identical with it.

This albuminous substance has received various names according to the structures in which it has been found, and the theory of its nature and uses which may have pre-

sented itself most strongly to the minds of its observers. In the bodies of the lowest animals, as the Rhizopoda or Gregarinida, of which it forms the greater portion, it has been called "sarcode," from its chemical resemblance to the flesh of the higher animals. When discovered in vegetable cells, and supposed to be the prime agent in their construction, it was termed "protoplasm." As the presumed formative matter in animal tissues it was called "blastema;" and, with the belief that wherever found, it alone of all matters has to do with generation and nutrition, Dr. Beale has surnamed it "germinal matter."

So far as can be discovered, there is no difference in chemical composition between the protoplasm of one part or organism and that of another. The movements which can be seen in certain vegetable cells apparently belong to a substance which is identical in composition with that which constitutes the greater portion of the bodies of the lowest animals, and which is present in greater or less quantity in all the living parts of the highest. So much appears to be a fact;—that in all living parts there exists an albuminous substance, in which in favourable cases for observation in vegetable and the lower animal organisms, there can be noticed certain phenomena which are not to be accounted for by physical impressions from without, but are the result of inherent properties we call *vital*. For example, if a hair of the Tradescantia Virginica, or of many other plants, be examined under the microscope, there is seen in each individual cell a movement of the protoplasmic contents in a certain definite direction around the interior of the cell. Each cell is a closed sac or bag, and its contents are therefore quite cut off from the direct influence of any motive power from without. The motion of the particles, moreover, in a circuit around the interior of the cell, precludes the notion of its being due to any other than those molecular changes which we call vital. Again, *in the lowest* animals, whose bodies resemble more than

anything else a minute mass of jelly, and which appear to be made up almost solely of this albuminous protoplasm, there are movements in correspondence with the needs of the organism, whether with respect to seizing food or any other purpose, which are unaccountable according to any known physical laws, and can only be called vital. In many, too, there is a kind of molecular current, exactly resembling that which is seen in a vegetable cell.

In the higher animals, phenomena such as these are so subordinate to the more complex manifestations of life that they are apt to be overlooked; but they exist nevertheless. The mere nutrition of each part of the body in man or in the higher animals, is performed after a fashion which is strictly analogous to that which holds good in the case of a vegetable cell, or a rhizopod; or, in other words, the life of each anatomical element in a complex structure, like the human body, resembles very closely the life of what in the lowest organisms constitutes the whole being. For example, the thin scaly covering or *epidermis*, which forms the outer part of a man's skin, is made up of minute cells, which, when living, are composed in part of protoplasm, and which are continually wearing away and being replaced by new similar elements from beneath; and this process of quick waste and repair could only take place under the very complex conditions of nutrition which exist in man. One working part of the organism of an animal is so inextricably interwoven with that of another, that any want or defect in one, is soon or immediately felt by the whole; and the epidermis, which only subserves a mechanical function, would be altered very soon by any defect in the more essential parts concerned in circulation, respiration, &c. But if we take simply the life-history of one of the small cells which constitute the epidermis, we find that it absorbs nourishment from the parts around, grows, and developes in a manner analogous to that which

belongs to a cell which constitutes part of a vegetable structure, or even a cell which by itself forms an independent being.

Remembering, however, the invariable presence of a living albuminous matter or protoplasm of apparently identical composition in all living tissues, animal and vegetable, we must not forget that its relations to the parts with which it is incorporated are still very doubtfully known; and all theories concerning it must be considered only tentative and of uncertain stability.

Among the anatomical elements of the human body, some appear, even with the help of the best microscopic apparatus, perfectly uniform and simple: they show no trace of structure, *i.e.*, of being composed of definitely arranged dissimilar parts. These are named *simple, structureless,* or *amorphous* substances. Such is the simple membrane which forms the walls of most primary cells, of the finest gland-ducts, and of the sarcolemma of muscular fibre; and such is the membrane enveloping the vitreous humour of the eye. Such also, having a dimly granular appearance, but no really granular structure, is the intercellular substance of the so-called *hyaline* cartilage.

In the parts which present determinate structure, certain primary forms may be distinguished, which, by their various modifications and modes of combination make up the tissues and organs of the body. Such are, 1. *Granules* or *molecules*, the simplest and minutest of the primary forms. They are particles of various sizes, from immeasurable minuteness to the 10,000th of an inch in diameter; of various and generally uncertain composition, but usually so affecting light transmitted through them, that at different focal distances their centre, or margin, or whole substance, appears black. From this character, as well as from their low specific gravity (for in microscopic examinations they always appear lighter than water), and from their solubility in ether when they can be favourably

tested, it is probable that most granules are formed of fatty or oily matter; or, since they do not coalesce as minute drops of oil would, that they are particles of oil coated over with albumen deposited on them from the fluid in which they float. In any fluid that is not too viscid, they exhibit the phenomenon of *molecular motion*, shaking and vibrating incessantly, and sometimes moving through the fluid, probably, in great measure, under the influence of external vibration.

Granules may be either *free*, as in milk, chyle, milky serum, yelk-substance, and most tissues containing cells with granules; or *enclosed*, as are the granules in nerve-corpuscles, gland-cells, and epithelium-cells, the pigment granules in the pigmentum nigrum and medullary substance of the hair; or *imbedded*, as are the granules of phosphate and carbonate of lime, in bones and teeth.

2. *Nuclei*, or *cytoblasts* (fig. 1, *b*), appear to be the simplest elementary structures, next to granules. They were thus named in accordance with the hypothesis that they are always connected with cells, or tissues formed from cells, and that in the development of these, each nucleus is the germ or centre around which the cell is formed. The hypothesis is only partially true, but the terms based on it are too familiarly accepted to make it advisable to change them till some more exact and comprehensive theory is formed.

Of the corpuscles called nuclei some are minute cellules or vesicles, with walls formed of simple membrane, enclosing often one or more particles, like minute granules, called *nucleoli* (fig. 1, *c*). Other nuclei, again, appear to be simply small masses of protoplasm, with no trace of vesicular structure.

One of the most general characters of the nucleus, and the most useful in microscopic examinations, is, that it is neither dissolved nor made transparent by acetic acid, but

acquires, when that fluid is in contact with it, a darker and more distinct outline. It is commonly, too, the part of the mature cell which is capable of being stained by an ammoniacal solution of carmine—the test, it may be remarked, by which, according to Dr. Beale, protoplasm or germinal matter may be always known.

Nuclei may be either *free* or *attached*. *Free nuclei* are such as either float in fluid, like those in some of the secretions, which appear to be derived from the secreting cells of the glands, or lie loosely imbedded in solid substance, as in the grey matter of the brain and spinal cord, and most abundantly in some quickly-growing tumours. *Attached nuclei* are either closely imbedded in homogeneous pellucid substance, as in rudimental cellular tissue; or are fixed on the surface of fibres, as on those of organic muscle- and organic nerve-fibres; or are enclosed in cells, or in tissues formed by the extension or junction of cells. Nuclei enclosed in cells appear to be attached to the inner surface of the cell-wall, projecting into the cavity. Their position in relation to the centre or axis of the cell is uncertain; often when the cell lies on a flat or broad surface, they appear central, as in blood corpuscles, epithelium-cells, whether tesselated or cylindrical; but, perhaps, more often their position has no regular relation to the centre of the cell. In most instances, each cell contains only a single nucleus; but in cartilage, especially when it is growing or ossifying, two or more nuclei in each cell are common; and the development of new cells is often effected by a division or multiplication of nuclei in the cavity of a parent cell; as in the primary blood-cells of the embryo, in the germinal vesicle, and others.

When cells extend and coalesce, so that their walls form tubes or sheaths, the nuclei commonly remain attached to the inner surface of the wall. Thus they are seen imbedded in the walls of the minutest capillary blood-vessels of, for example, the retina and brain; in the sarcolemma of

transversely striated muscular fibres; and in minute gland-tubes.

Nuclei are most commonly oval or round, and do not generally conform themselves to the diverse shapes which the cells assume; they are altogether less variable elements, even in regard to size, than the cells are, of which fact one may see a good example in the uniformity of the nuclei in cells so multiform as those of epithelium. But sometimes they appear to be developed into filaments, elongating themselves and becoming solid, and uniting end to end for greater length, or by lateral branches to form a network. So, according to Henle, are formed the filaments of the striated and fenestrated coats of arteries; and, according to Beale, the so-called connective tissue corpuscles are to be considered branched nuclei, formed of protoplasm or germinal matter.

3. *Cells.*—The word "cell" of course implies strictly a hollow body, and the term was a sufficiently good one when all so-called cells were considered to be small bags with a membranous envelope, and more or less liquid contents. Many bodies, however, which are still called cells do not answer to this description, and the term therefore, if taken in its literal signification, is very apt to lead astray, and, indeed, very frequently does so. It is too widely used, however, to be given up, at least for the present, and we must therefore consider the term to indicate, either a membranous closed bag with more or less liquid contents, and almost always a nucleus; or a small semi-solid mass of protoplasm, with no more definite boundary-wall than such as has been formed by a condensation of its outer layers, but with, most commonly, a small granular substance in the centre, called, as in the first place, a nucleus. In both cases the nucleus may contain a nucleolus. Fat cells (fig. 11) are examples of the first kind of cells; white blood-corpuscles (fig. 26) of the second.

The cell-wall, when there is one, never presents any

appearance of structure: it appears sometimes to be an albuminous substance; sometimes a horny matter, as in thick and dried cuticle. In almost all cases (the dry cells of horny tissue, perhaps, alone excepted) the cell-wall is made transparent by acetic acid, which also penetrates into the interior and distends it, so that it can hardly be discerned. But in such cases the cell-wall is usually not dissolved; it may be brought into view again by merely neutralizing the acid with soda or potash.

The simplest *shape* of cells, and that which is probably the normal shape of the primary cell, is oval or spheroidal, as in cartilage-cells and lymph-corpuscles; but in many instances they are flattened and discoid, as in the red blood-corpuscles (fig. 26) or scale-like, as in the epidermis and tesselated epithelium (fig. 2). By mutual pressure they may become many-sided, as are most of the pigment-cells of the choroidal pigmentum nigrum (fig. 12), and those in close-textured adipose tissue; they may assume a conical or cylindriform or prismatic shape, as in the varieties of cylinder-epithelium (fig. 4); or be caudate, as in certain bodies in the spleen; they may send out exceedingly fine processes in the form of vibratile cilia (fig. 6), or larger processes, with which they become stellate, or variously caudate, as in some of the ramified pigment-cells of the choroid coat of the eye (fig. 13).

The *contents* of all living cells, including the nucleus, are formed in a greater or less degree of protoplasm,—less as the cell grows older. But, besides, cells contain matters almost infinitely various, according to the position, office, and age of the cell. In adipose tissue they are the oily matter of the fat; in gland-cells, the contents are the proper substance of the secretion, bile, semen, etc., as the case may be; in pigment cells they are the pigment granules that give the colour; and in the numerous instances in which the cell-contents can be neither seen because they are pellucid, nor tested because of their minute quantity,

they are yet, probably, peculiar in each tissue, and constitute the greater part of the proper substance of each. Commonly, when the contents are pellucid, they contain granules which float in them; and when water is added and the contents are diluted, the granules display an active molecular movement within the cavity of the cell. Such a movement may be seen by adding water to mucus-, or granulation-corpuscles, or to those of lymph. In a few cases, the whole cavity of the cell is filled with granules: it is so in yelk-cells and milk-corpuscles, in the large diseased corpuscles often found among the products of inflammation, and in some cells when they are the seat of extreme fatty degeneration. All cells containing abundant granules appear to be either lowly organized, as for nutriment, *e.g.*, yelk-cells, or degenerate, *e.g.*, granule-cells of inflammation, or of mucus. The peculiar contents of cells may be often observed to accumulate first around or directly over the nuclei, as in the cells of black pigment, in those of melanotic tumours, and in those of the liver during the retention of bile.

Intercellular substance is the material in which, in certain tissues, the cells are imbedded. Its quantity is very variable. In the finer epithelia, especially the columnar epithelium on the mucous membrane of the intestines, it can be just seen filling the interstices of the close-set cells; here it has no appearance of structure. In cartilage and bone, it forms a large portion of the whole substance of the tissue, and is either homogeneous and finely granular (fig. 14), or osseous, or, as in fibro-cartilage, resembles fine fibrous tissue (fig. 15). In some cases, the cells are very loosely connected with the intercellular substance, and may be nearly separated from it, as in fibro-cartilage: but in some their walls seem amalgamated with it.

The foregoing may be regarded as the simplest, and the nearest to the primary forms assumed in the organization of animal matter; as the states into which this passes in

becoming a solid tissue living or capable of life. By the further development of tissue thus far organized, higher or secondary forms are produced, which it will be sufficient in this place merely to enumerate. Such are,

4. *Filaments*, or *fibrils*.—Threads of exceeding fineness, from $\frac{1}{20000}$th of an inch upwards. Such filaments are cylindriform, as are those of the striated muscular and the fibro-cellular or areolar tissue (fig. 8); or flattened, as are those of the organic muscles. Filaments usually lie in parallel fasciculi, as in muscular and tendinous tissues; but in some instances are matted or reticular with branches and intercommunication, as are the filaments of the middle coat, and of the longitudinally-fibrous coat of arteries; and in other instances, are spirally wound, or very tortuous, as in the common fibro-cellular-tissue (fig. 9).

5. *Fibres* in the instances to which the name is commonly applied are larger than filaments or fibrils, but are by no essential general character distinguished from them. The flattened band-like fibres of the coarser varieties of organic muscle or elastic tissue (fig. 10) are the simplest examples of this form; the toothed fibres of the crystalline lens are more complex; and more compound, so as hardly to permit of being classed as elementary forms, are the striated muscular fibres, which consist of bundles of filaments enclosed in separate membranous sheaths, and the cerebro-spinal nerve-fibres, in which similar sheaths enclose apparently two varieties of nerve substance.

6. *Tubules* are formed of simple, or structureless membrane, such as the investing sheaths of striated muscular and cerebro-spinal nerve-fibres, and the basement membrane or proper wall of the fine ducts of secreting glands; or they may be formed, as in the case of the minute capillary lymph and blood-vessels, by the apposition, edge to edge, in a single layer, of variously shaped flattened cells (fig. 48).

With these simple materials, the various parts of the

body are built up; the more elementary tissues being, so to speak, first compounded of them; while these again are variously mixed and interwoven to form more intricate combinations. Thus are constructed epithelium and its modifications, connective tissue, fat, cartilage, bone, the fibres of muscle and nerve, etc.; and these again, with the more simple structures before mentioned, are used as materials wherewith to form arteries, veins, and lymphatics, secreting and vascular glands, lungs, heart, liver, and other parts of the body.

CHAPTER IV.*

STRUCTURE OF THE ELEMENTARY TISSUES.

Epithelium.

ONE of the simplest of the elementary structures of which the human body is made up, is that which has received the name of *Epithelium*. Composed of nucleated cells which are arranged most commonly in the form of a continuous membrane, it lines the free *surfaces* both of the inside and outside of the body, and its varieties, with one exception, have been named after the shapes which the individual cells in different parts assume. Classified thus, Epithelium presents itself under four principal forms, the characters of each of which are distinct enough in well-marked examples; but when, as frequently happens, a continuous

* The following Chapter, containing an outline-description of the elementary tissues, has been inserted for the convenience of students. For a much fuller and better account, the reader may be referred to Dr. Sharpey's admirable descriptions in Quain's Anatomy.

surface possesses at different parts two or more different epithelia, there is a very gradual transition from one to the other.

1. The first and most common variety is the *squamous* or *tesselated* epithelium (figs. 1 and 2), which is composed of flat, oval, roundish, or polygonal nucleated cells, of various size, arranged in one, or in many superposed layers. Arranged in several superposed layers this form of

Fig. 1.*

Fig. 2.†

epithelium covers the skin, where it is called the *Epidermis*, and is spread over the mouth, pharynx, and œsophagus, the conjunctiva covering the eye, the vagina, and entrance of the urethra in both sexes; while, as a single layer the same kind of epithelium lines the interior of most of the serous and synovial sacs, and of the heart, blood-vessels, and lymph-vessels.

2. Another variety of epithelium named *spheroidal*, from the usually more or less rounded outline of the cells com-

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* Fig. 1. Fragment of epithelium from a serous membrane (peritoneum); magnified 410 diameters. *a*. cell; *b*. nucleus; *c*. nucleoli (Henle).

† Fig. 2. Epithelium scales from the inside of the mouth; magnified 260 diameters (Henle).

posing it (*d*, fig. 3), is found chiefly lining the interior of the ducts of the compound glands, and more or less completely filling the small sacculations or acini, in which they terminate. It commonly indeed occupies the true secreting parts of all glands, and hence is sometimes called *glandular* epithelium (*b*, *c*, and *d*, fig. 3). Often, from mutual pressure,

Fig. 3.*

the cells acquire a polygonal outline. From the fact, however, of the term *spheroidal* epithelium being a generic one for almost all gland-cells, the shapes and sizes of the cells composing this variety of epithelium are, as might be expected, very diverse in different parts of the body.

3. The third variety is the *cylindrical* or *columnar*

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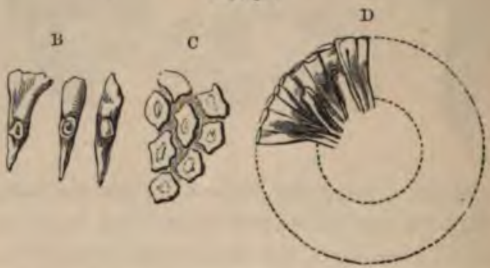
* Fig. 3. The gastric glands of the human stomach (magnified). *a*, deep part of a pyloric gastric gland (from Kölliker); the cylindrical epithelium is traceable to the cæcal extremities. *b* and *c*, cardiac gastric glands (from Allen Thomson); *b*, vertical section of a small portion of the mucous membrane with the glands magnified 30 diameters; *c*, deeper portion of one of the glands, magnified 65 diameters, showing a slight division of the tubes, and a sacculated appearance produced by the large glandular cells within them; *d*, cellular elements of the cardiac glands magnified 250 diameters.

epithelium (figs. 4 and 5), which extends from the cardiac orifice of the stomach along the whole of the digestive canal to the anus, and lines the principal gland-ducts which

Fig. 4.*

open upon the mucous surface of this tract, sometimes throughout their whole extent (*a*, fig. 3), but in some cases only at the part nearest to the orifice (*b* and *c*). It is also

Fig. 5.†



found in the gall-bladder and in the greater portion of the urethra, and in some other parts, as the duct of the parotid gland and of the testicle. It is composed of oblong cells closely packed, and placed perpendicularly to the surface they cover, their deeper or attached extremities being most

* Fig. 4. Cylindrical epithelium from intestinal villus of a rabbit; magnified 300 diameters (from Kölliker).

† Fig. 5. Cylinders of the intestinal epithelium (after Henle):— B. from the jejunum; C. cylinders of the intestinal epithelium as seen when looking on their free extremities; D. ditto, as seen on a transverse section of a villus.

commonly smaller than those which are free. Each of such cells encloses, at nearly mid distance between its base and apex, a flat nucleus with nucleoli (B, fig. 5); the nuclei being arranged at such heights in contiguous cells as not to interfere with each other by mutual pressure.

4. In the fourth variety of epithelium cells, usually *cylindrical*, but occasionally of some other shape, are provided at their free extremities with several fine pellucid pliant processes or cilia (figs. 6 and 7). This form of epithelium lines the whole respiratory tract of mucous membrane and its prolongations. It occurs also in some parts

*Fig. 6.**

Fig. 7.†

of the generative apparatus; in the male, lining the *vasa efferentia* of the testicle, and their prolongations as far as the lower end of the *epididymis;* and, in the female commencing about the middle of the neck of the uterus, and extending to the fimbriated extremities of the Fallopian tubes, and for a short distance along the peritoneal surface of the latter. A *tesselated* epithelium, with scales partly covered with cilia, lines, in great part, the interior of the cerebral ventricles, and of the minute central canal of the spinal cord.

If a portion of ciliary mucous membrane from a living or recently dead animal be moistened and examined with a microscope, the cilia are observed to be in constant motion,

* Fig. 6. Spheroidal ciliated cells from the mouth of the frog; magnified 300 diameters (Sharpey).

† Fig. 7. Columnar ciliated epithelium cells from the human nasal membrane; magnified 300 diameters (Sharpey).

moving continually backwards and forwards, and alternately rising and falling with a lashing or fanning movement. The appearance is not unlike that of the waves in a field of corn, or swiftly running and rippling water. The general result of their movements is to produce a continous current in a determinate direction, and this direction is invariably the same on the same surface, being usually in the case of a cavity towards its external orifice.

Uses of Epithelium.—The various kinds of epithelium serve one general purpose, namely, that of protecting, and at the same time rendering smooth, the surfaces on which they are placed. But each, also, discharges a special office in relation to the particulr function of the membrane on which it is placed.

In mucous and synovial membranes it is highly probable that the epithelium-cells, whatever be their forms and whatever their other functions, are the organs in which by a regular process of elaboration and secretion, such as will be afterwards described, *mucus* and synovial fluid are formed and discharged. (See chapter on Secretion.)

Ciliated epithelium has another superadded function. By means of the current set up by its cilia in the air or fluid in contact with them, it is enabled to propel the fluids or minute particles of solid matter, which come within the range of its influence, and aid in their expulsion from the body. In the respiratory tract of mucous membrane the current set up in the air may also assist in the diffusion and change of gases, on which the due aëration of the blood depends. In the Fallopian tube the direction of the current excited by the cilia is towards the cavity of the uterus, and may thus be of service in aiding the progress of the ovum. Of the purposes served by the cilia which line the ventricles of the brain nothing is known.

The nature of ciliary motion and the circumstances by

which it is influenced will be considered hereafter. (See chapter on Motion.)

Epithelium is devoid of blood-vessels, and lymphatics. The cells composing it are nourished by absorption of nutrient matter from the tissues on which they rest; and as they grow old they are cast off and replaced by new cells from beneath.

Areolar, Cellular, or Connective Tissue.

This tissue, which has received various names according to the qualities which seemed most important to the authors who have described it, is met with in some form or other in every region of the body; the areolar tissue of one district being, directly or indirectly, continuous with that of

Fig. 8.*

all others. In most parts of the body this structure contains fat, but the quantity of the latter is very variable, and in some few regions it is absent altogether (p. 38).

* Fig. 8. Filaments of areolar tissue, in larger and smaller bundles, as seen under a magnifying power of 400 diameters (Sharpey).

Probably no nerves are distributed to areolar tissue itself, although they pass through it to other structures; and although blood-vessels are supplied to it, yet they are sparing in quantity, if we except those destined for the fat which is held in its meshes.

Under the microscope areolar tissue seems composed of a mesh-work of fine fibres of two kinds. The first, which makes up the greater part of the tissue, is formed of very fine white structureless fibres, arranged closely in bands and bundles, of wave-like appearance when not stretched out, and crossing and intersecting in all directions (fig. 8). The second kind, or the yellow elastic fibre (fig. 10), has a much

*Fig. 9.**

sharper and darker outline, and is not arranged in bundles, but intimately mingled with the first variety, as more or less separate and well-defined fibres, which twist among and around the bundles of white filaments (fig. 9). Sometimes

* Fig. 9. Magnified view of areolar tissues (from different parts) treated with acetic acid. The white filaments are no longer seen, and the yellow or elastic fibres with the nuclei come into view. At *c*, elastic fibres wind round a bundle of white fibres, which, by the effect of the acid, is swollen out between the turns. Some connective tissue *corpuscles* are indistinctly represented in *c* (Sharpey).

the yellow fibres divide at their ends and anastomose with each other by means of the branches. Among the fibrous parts of areolar or connective tissue are little nuclear bodies of various shapes, called *connective-tissue corpuscles* (fig. 9, *c.*), some of which are prolonged at various points of their outline into small processes which meet and join others like them proceeding from their neighbours.

The chief functions of areolar tissue seem to consist in the investment and mechanical support of various parts, and as a connecting bond between such structures as may need it. The connective-tissue corpuscles, which, according to Beale, are small branched particles of germinal matter or protoplasm, probably minister to the nutrition of the texture in which they are seated.

Fig. 10.*

In various parts of the body, each of the two constituents of areolar tissue which have been just mentioned, may exist separately, or nearly so. Thus tendons, fasciæ, and the like more or less inelastic structures, are formed almost exclusively of the white fibrous tissue, arranged according to the purpose required, either in parallel bundles or membraneous meshes; while the yellow elastic fibres are found to make up almost alone such elastic structures as the vocal cords, the ligamenta subflava, etc., and to enter largely into the composition of the blood-vessels, the trachea, the lungs, and many other parts of the body.

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* Fig. 10. Elastic fibres from the ligamenta subflava, magnified about 200 diameters (Sharpey).

Adipose Tissue.

In almost all regions of the human body a larger or smaller quantity of *adipose* or *fatty* tissue is present; the chief exceptions being the subcutaneous tissue of the eyelids, penis and scrotum, the nymphæ and the cavity of the cranium. Adipose tissue is also absent from the substance of many organs, as the lungs, liver and others.

Fatty matter, not in the form of a distinct tissue, is also widely present in the body, as the fat of the liver and brain, of the blood and chyle, etc.

Adipose tissue is almost always found seated in areolar tissue, and forms in its meshes little masses of unequal size and irregular shape, to which the term, lobules, is commonly applied. Under the microscope it is found to

Fig. 11.*

consist essentially of little vesicles or cells about $\frac{1}{400}$th or $\frac{1}{500}$th of an inch in diameter, each composed of a structureless and colourless membrane or bag, filled with fatty matter which is liquid during life, but in part solidified after death. A nucleus is always present in some part or other of the cell-wall; but in the ordinary condition of the

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* Fig. 11. A small cluster of fat-cells; magnified 150 diameters (Sharpey).

cell it is not easily or always visible. The ultimate cells are held together by capillary blood-vessels; while the little clusters thus formed are grouped into small masses, and held so, in most cases, by areolar tissue. The oily matter contained in the cells is composed chiefly of the compounds of fatty acids with glycerin, which are named olein, stearin, and palmitin.

It is doubtful whether lymphatics or nerves are supplied to fat, although both pass through it on their way to other structures.

Among the uses of fat, these seem to be the chief:—

1. It serves as a store of combustible matter which may be re-absorbed into the blood when occasion requires, and being burnt, may help to preserve the heat of the body.

2. That part of the fat which is situate beneath the skin must, by its want of conducting power, assist in preventing undue waste of the heat of the body by escape from the surface.

3. As a packing material, fat serves very admirably to fill up spaces, to form a soft and yielding yet elastic material wherewith to wrap tender and delicate structures, or form a bed with like qualities on which such structures may lie, unendangered by pressure. As good examples of situations in which fat serves such purposes may be mentioned the palms of the hands, and soles of the feet, and the orbits.

4. In the long bones, fatty tissue, in the form known as marrow, serves to fill up the medullary canal, and to support the small blood vessels which are distributed from it to the inner part of the substance of the bone.

Pigment.

In various parts of the body there exists a considerable quantity of dark pigmentary matter, *e.g.*, in the choroid coat of the eye, at the back of the iris, in the skin, etc.

In all these cases the dark colour is due to the presence of so-called pigment-cells.

Pigment-cells are for the most part polyhedral (fig. 12) or spheroidal, although sometimes they have irregular processes, as shown in fig. 13. The cell-wall itself is colourless,—the dark tint being produced by small dark granules heaped closely together, and more or less concealing the nucleus, itself colourless, which each cell contains. The dark tint of the skin, in those of dark complexion and in the coloured races, is seated chiefly in the

Fig. 12.*

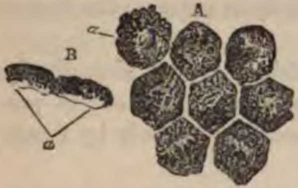


Fig. 13.†

epidermis, and depends on the presence of pigment-cells, which, except in the presence of the dark granules in their interior, closely resemble the colourless cells with which they are mingled. The pigment-cells are situate chiefly in the deep layer of the epidermis, or the so-called *rete m ucosum* (see chapter on the Skin).

* Fig. 12. Pigment-cells from the choroid; magnified 370 diameters (Henle). A, cells still cohering, seen on their surface; *a*, nucleus indistinctly seen. In the other cells the nucleus is concealed by the pigment granules. B, two cells seen in profile; *a*, the outer or posterior art containing scarcely any pigment.

† Fig. 13. Ramified pigment cells, from the tissue of the choroid coat of the eye; magnified 350 diameters (after Kölliker). *a*, cells with pigment; *b*, colourless fusiform cells.

The pigmentary matter is a very insoluble compound of carbon, hydrogen, nitrogen and oxygen,—the carbon largely predominating; besides, there is a small quantity of saline matter.

The uses of pigment in most parts of the body are not clear. In the eyeball it is evidently intended for the absorption of superfluous rays of light.

Cartilage.

Cartilage or gristle exists in different forms in the human body, and has been classified under two chief heads, namely, *temporary* and *permanent* cartilage; the former term being applied to that kind of cartilage which, in the fœtus and in young subjects, is destined to be converted into bone. The varieties of permanent cartilage have been arranged in three classes, namely, the *cellular*, the *hyaline*, and the *fibrous* cartilages,—the last-named, being again capable of subdivision into two kinds, namely, *elastic* or yellow cartilage, and the so-called *fibro-cartilage*.

Elastic cartilage, however, contains fibres, and fibro-cartilage is more or less elastic; it will be well, therefore, for distinction's sake to term those two kinds *white* fibro-cartilage and *yellow* fibro-cartilage respectively.

The accompanying table represents the classification of the varieties of cartilage:—

1. Temporary.		
2. Permanent.	A. Cellular.	
	B. Hyaline.	
	C. Fibrous.	White fibro-cartilage.
		Yellow fibro-cartilage.

All kinds of cartilage are composed of cells imbedded in a substance called the *matrix:* and the apparent differences of structure met with in the various kinds of cartilage are more due to differences in the character of the *matrix* than of the cells. Among the latter, however, there is also considerable diversity of form and size.

With the exception of the articular variety, cartilage is invested by a thin but tough and firm fibrous membrane called the *perichrondrium*. On the surface of the articular cartilage of the fœtus, the perichondrium is represented by a film of epithelium; but this is gradually worn away up to the margin of the articular surfaces, when by use the parts begin to suffer friction.

1. *Cellular* cartilage may be readily obtained from the external ear of rats, mice, or other small mammals. It is composed almost entirely of cells (hence its name), with little or no matrix. The latter, when present, consists of very fine fibres, which twine about the cells in various directions and enclose them in a kind of network. The cells are packed very closely together,—so much so that it is not easy in all cases to make out the fine fibres often encircling them.

Cellular cartilage is found in the human subject, only in early fœtal life, when it constitutes the *Chorda dorsalis* (see chapter on Generation).

Fig. 14.*

2. *Hyaline* cartilage is met with largely in the human body,—investing the articular ends of bones, and forming the costal cartilages, the nasal cartilages, and those of the larynx, with the exception of the *epiglottis* and *cornicula laryngis*. Like other cartilages it is composed of cells imbedded in a *matrix* (fig. 14).

* Fig. 14. A thin layer peeled off from the surface of the cartilage of the head of the humerus, showing flattened groups of cells. The shrunken cell-bodies are distinctly seen, but the limits of the capsular cavities, where they adjoin one another, are but faintly indicated. *Magnified* 400 diameters (after Sharpey).

The cells, which contain a nucleus with nucleoli, are irregular in shape, and generally grouped together in patches. The patches are of various shapes and sizes, and placed at unequal distances apart. They generally appear flattened near the free surface of the mass of cartilage in which they are placed, and more or less perpendicular to the surface in the more deeply seated portions.

The matrix in which they are imbedded has a dimly granular appearance, like that of ground glass.

In the hyaline cartilage of the ribs, the cells are mostly larger than in the articular variety, and there is a tendency to the development of fibres in the matrix. The costal cartilages also frequently become ossified in old age, as also do some of those of the larynx.

Temporary cartilage closely resembles the ordinary hyaline kind; the cells, however, are not grouped together after the fashion just described, but are more uniformly distributed throughout the *matrix*.

Articular hyaline cartilage is reckoned among the so-called *non-vascular* structures, no blood-vessels being supplied directly to its own substance; it is nourished by those of the bone beneath. When hyaline cartilage is in thicker masses, as in the case of the cartilages of the ribs, a few blood-vessels traverse its substance. The distinction, however, between all so-called *vascular* and *non-vascular* parts, is at the best a very artificial one (see chapter on Nutrition).

Nerves are probably not supplied to any variety of cartilage.

Fibrous cartilage, as before mentioned, occurs under two chief forms, the *yellow* and the *white* fibro-cartilage.

Yellow fibro-cartilage is found in the external ear, in the epiglottis and cornicula laryngis, and in the eyelid. The cells are rounded or oval, with well-marked nuclei and nucleoli. The matrix in which they are seated is composed almost entirely of fine fibres, which form an intricate inter-

lacement about the cells, and in their general characters are allied to the yellow variety of fibrous tissue (fig. 15).

Fig. 15.*

White fibro-cartilage, which is much more widely distributed throughout the body, than the foregoing kind, is composed like it, of cells and a matrix; the latter, however, being made up almost entirely of fibres closely resembling those of white fibrous tissue.

In this kind of fibro-cartilage it is not unusual to find a great part of its mass composed almost exclusively of fibres, and deserving the name of cartilage only from the fact that in another portion, continuous with it, cartilage cells may be pretty freely distributed.

The different situations in which white fibro-cartilage is formed have given rise to the following classification:—

1. *Inter-articular* fibro-cartilage, *e.g.*, the semilunar cartilages of the knee-joint.

2. *Circumferential* or *marginal*, as on the edges of the acetabulum and glenoid cavity of the scapula.

3. *Connecting*, *e.g.*, the inter-vertebral fibro-cartilages.

4. Fibro-cartilage is found in the sheaths of tendons, and sometimes in their substance. In the latter situation, the nodule of fibro-cartilage is called a *sesamoid* fibro-cartilage, of which a specimen may be found in the tendon of the tibialis posticus, in the sole of the foot, and usually in the neighbouring tendon of the peroneus longus.

The *uses* of cartilage are the following;—in the joints, to form smooth surfaces for easy friction, and to act as a *buffer*, in shocks; to bind bones together, yet to allow a certain degree of movement, as between the vertebræ; to

* Fig. 15. Section of the epiglottis, magnified 380 diameters (Dr. *Baly*).

form a firm framework and protection, yet without undue stiffness or weight, as in the larynx and chest walls; to deepen joint-cavities, as in the acetabulum, yet not so as to restrict the movements of the bones; to be, where such qualities are required, firm, tough, flexible, elastic, and strong.

Structure of Bones and Teeth.

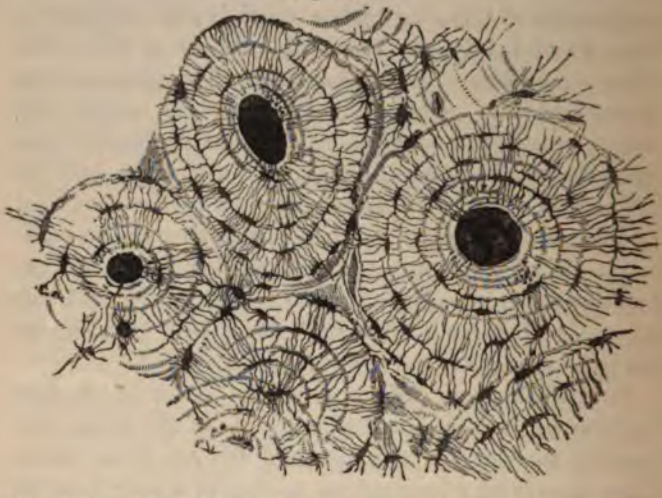
Bone is composed of *earthy* and *animal* matter in the proportion of about 67 per cent. of the former to 33 per cent. of the latter. The earthy matter is composed chiefly of *phosphate* of lime, but besides there is a small quantity, about 11 of the 67 per cent., of *carbonate* of lime, with minute quantities of some other salts. The animal matter is resolved into gelatine by boiling. The earthy and animal constituents of bone are so intimately blended and incorporated the one with the other, that it is only by chemical action, as for instance, by heat in one case, and by the action of acids in another, that they can be separated. Their close union, too, is further shown by the fact that when by acids the earthy matter is dissolved out, or, on the other hand, when the animal part is burnt out, the general shape of the bone is alike preserved.

To the naked eye there appear two kinds of structure in different bones, and in different parts of the same bone, namely, the *dense* or *compact*, and the *cancellous* tissue. Thus, in making a longitudinal section of a long bone, as the humerus or femur, the articular extremities are found capped on their surface by a thin shell of *compact* bone, while their interior is made up of the spongy or *cancellous* tissue. The *shaft*, on the other hand, is formed almost entirely of a thick layer of the *compact* bone, and this surrounds a central canal, the *medullary* cavity—so called from its containing the *medulla* or *marrow* (p. 39). In the flat bones, as the parietal bone or the scapula, one layer of the cancellous structure lies between two layers of the compact tissue, and in the short and irregular bones, as those of the *carpus* and *tarsus*, the cancellous tissue alone

fills the interior, while a thin shell of compact bone forms the outside. The spaces in the cancellous tissue are filled by a species of marrow, which differs considerably from that of the shaft of the long bones. It is more fluid, and of a reddish colour, and contains very few fat cells.

The surfaces of bones, except the parts covered with articular cartilage, are clothed by a tough fibrous membrane, the *periosteum;* and it is from the blood-vessels which are distributed first in this membrane, that the

Fig. 16.*



bones, especially their more compact tissue, are in great part supplied with nourishment,—minute branches from the periosteal vessels entering the little foramina on the surface of the bone, and finding their way to the Haversian canals, to be immediately described. The long bones are

* Fig. 16. Transverse section of compact tissue (of humerus) magnified about 150 diameters. Three of the Haversian canals are seen, with their concentric rings; also the corpuscles or lacunæ, with the canaliculi extending from them across the direction of the lamellæ. The Haversian apertures had got filled with débris in grinding down the section, and therefore appear black in the figure, which represents the *object as viewed* with transmitted light (after Sharpey).

supplied also by a proper nutrient artery, which entering at some part of the shaft so as to reach the medullary canal, breaks up into branches for the supply of the marrow, from which again small vessels are distributed to the interior of the bone. Other small blood-vessels pierce the articular extremities for the supply of the cancellous tissue.

Notwithstanding the differences of arrangement just mentioned, the structure of all bone is found, under the microscope, to be essentially the same. Examined with a rather high power, its substance is found occupied by a multitude of little spaces, called *lacunæ*, with very minute canals or *canaliculi*, as they are termed, leading from them, and anastomosing with similar little prolongations from other lacunæ (fig. 16). In very thin layers of bone, no other canals than these may be visible; but on making a transverse section of the compact tissue, *e.g.*, of a long bone, as the humerus or ulna, the arrangement shewn in fig. 16 can be seen. The bone seems mapped out into small circular districts, at or about the centre of each of which is a hole, and around this an appearance as of concentric layers—the *lacunæ* and *canaliculi* following the same concentric plan of distribution around the small hole in the centre, with which, indeed, they communicate. On making a longitudinal section, the central holes are found to be simply the cut extremities of small canals which run lengthwise through the bone (fig. 17), and

Fig. 17*

* Fig. 17. Haversian canals, seen in a longitudinal section of the compact tissue of the shaft of one of the long bones. *a.* Arterial canal *b.* Venous canal; *c.* Dilatation of another venous canal.

are called Haversian canals, after the name of the physician, Clopton Havers, who first accurately described them.

The Haversian canals, the average diameter of which is $\frac{1}{500}$ of an inch, contain blood-vessels, and by means of them, blood is conveyed to all, even the densest parts of the bone; the minute canaliculi and lacunæ absorbing nutrient matter from the Haversian blood-vessels, and conveying it still more intimately to the very substance of the bone which they traverse. The blood-vessels enter the Haversian canals both from without, by traversing the small holes which exist on the surface of all bones beneath the periosteum, and from within by means of small channels, which extend from the medullary cavity, or from the cancellous tissue. According to Todd and Bowman, the arteries and veins usually occupy separate canals, and the veins which are the larger, often present, at irregular intervals, small pouch-like dilatations (fig. 17).

The *lacunæ* are occupied by nucleated cells, or, as Dr. Beale expresses it, minute portions of protoplasm or germinal matter; and there is every reason to believe that the lacunar cells are homologous with the corpuscles of the connective tissue, each little particle of protoplasm ministering to the nutrition of the bone immediately surrounding it, and one lacunar particle communicating with another, and with its surrounding district, and with the blood-vessels of the Haversian canals, by means of the minute streams of fluid nutrient matter which occupy the *canaliculi*.

Besides the concentric *lamellæ* of bone tissue which surround the Haversian canal in the shaft of a long bone, are others, especially near the circumference, which surround the whole bone, and are arranged concentrically with regard to the medullary canal.

The ultimate structure of the *lamellæ* appears to be reticular. If a thin film be peeled off the surface of a bone from which the earthy matter has been removed by acid,

and examined with a high power of the microscope, it will be found composed, according to Sharpey, of a finely reticular structure, formed apparently of very slender fibres decussating obliquely, but coalescing at the points of intersection, as if here the fibres were fused rather than woven together (fig. 18).

Fig. 18.*

In many places these reticular lamellæ are perforated by tapering fibres, resembling in character the ordinary white or rarely the elastic fibrous tissue, which bolt the neighbouring lamellæ together, and may be drawn out when the latter are torn asunder (fig. 19).

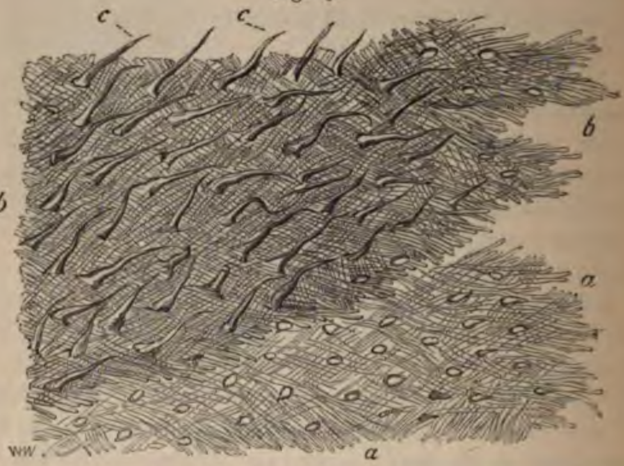
Bone is developed after two different fashions. In one, the tissue in which the earthy matter is laid down is a *membrane*, composed mainly of fibres and granular cells, like imperfectly developed connective-tissues. Of this kind of ossification in *membrane*, the flat bones of the skull are examples. In the other, and much more common case, of which a long bone may be cited as an instance, the ossification takes place in *cartilage*.

In most bones ossification begins at more than one point; and, from these *centres of ossification*, as they are called, the process of deposition of calcareous matter advances in all directions. Bones grow by constant development of the cartilage or membrane between these centres of ossification, until by the process of calcification advancing at a quicker rate than the development of the softer structures, the bone becomes impregnated through-

* Fig. 18. Thin layer peeled off from a softened bone, as it appears under a magnifying power of 400.—This figure, which is intended to represent the reticular structure of a lamella, gives a better idea of the object when held rather farther off than usual from the eye (from Sharpey).

out with calcareous matter, and can grow no more. In the long bones the main centres of ossification are seated at the middle of the shaft, and at each of the extremities. Increase of the *length* of bones, therefore, occurs at the part which intervenes between the ossifying centre in the shaft

Fig. 19.*



and that at each extremity; while increase in thickness takes place by the formation of layers osseous tissues beneath the *periosteum.* The former is an example of ossification in cartilage; the latter of ossification in membrane.

Teeth.—A tooth is generally described as possessing a *crown, neck,* and *fang* or *fangs.* The *crown* is the portion which projects beyond the level of the gum. The *neck* is that constricted portion just below the crown which is

* Fig. 19. Lamellæ torn off from a decalcified human parietal bone at some depth from the surface. *a*, a lamella, shewing reticular fibres; *b*, *b*, darker part, where several lamellæ are superposed; *c*, *c*, perforating fibres. Apertures through which perforating fibres had passed, are seen especially in the lower part, *a*, *a*, of the figure. Magnitude as seen under a power of 200, but not drawn to a scale (from a drawing by Dr. Allen Thomson).

embraced by the free edges of the gum, and the *fang* includes all below this.

On making a longitudinal section through the centre of a tooth (figs. 20 and 21), it is found to be principally composed of a hard matter, *dentine* or ivory; while in the centre this dentine is hollowed out into a cavity resembling in general shape the outline of the tooth, and called the

Fig. 20.*

pulp-cavity, from its containing a very vascular and sensitive little mass composed of connective tissue, blood-vessels and nerves, which is called the *tooth-pulp*. The pulp is continuous below, through an opening at the end of the fang, with the mucous membrane of the gum. Capping that part of the dentine which projects beyond the level of the gum, is a layer of very hard calcareous matter, the *enamel*, while sheathing the portion of dentine which is beneath the level of the gum, is a layer of true bone, called the *cement* or *crusta petrosa*. At the neck of the tooth the cement is exceedingly thin, but it gradually becomes thicker as it approaches and covers the lower end or apex of the fang.

Dentine or ivory in chemical composition closely resembles bone. It contains, however, rather less animal matter; the proportion in 100 parts being about 28 of *animal* matter to 72 of *earthy*. The former, like the animal matter of bone, may be resolved into gelatin by boiling. The

* Fig. 20. Sections of an Incisor and Molar Tooth.—The longitudinal sections show the whole of the pulp-cavity in the incisor and molar teeth, its extension upwards within the crown, and its prolongation downwards into the fangs, with the small aperture at the point of each; these and the cross section show the relation of the dentine and enamel.

earthy matter is made up chiefly of phosphate of lime, with a small portion of the carbonate, and traces of some other salts.

Fig. 21.*

Under the microscope, dentine is seen to be finely channelled by a multitude of fine tubes, which, by their inner ends, communicate with the pulp-cavity, and by their outer extremities come into contact with the under part of the enamel and cement, and sometimes even penetrate them for a greater or less distance. In their course from the pulp-cavity to the surface of the dentine, these minute tubes form gentle and nearly parallel curves, and divide and subdivide dichotomously, but without much lessening of their calibre until they are approaching their peripheral termination. From their sides proceed other exceedingly minute secondary canals, which extend into the dentine between the tubules.

The tubules of the dentine, the average diameter of which at their inner and larger extremity is $\frac{1}{4500}$ of an inch, contain fine prolongations from the *tooth-pulp* which give the dentine a certain faint sensitiveness under ordinary circumstances, and, without doubt, have to do also with its nutrition.

* Fig. 21. Magnified Longitudinal Section of a Bicuspid Tooth (after Retzius)—1, the ivory or dentine, showing the direction and primary curves of the dental tubuli; 2, the pulp-cavity, with the small apertures of the tubuli into it; 3, the cement or crusta petrosa, covering the fang as high as the border of the enamel at the neck, exhibiting lacunæ; 4, the enamel resting on the dentine; this has been worn away by use from the upper part.

The *enamel*, which is by far the hardest portion of a tooth, is composed, chemically, of the same elements that enter into the composition of dentine and bone. Its animal matter, however, amounts only to about 2 or 3 per cent.

Examined under the microscope, enamel is found composed of fine hexagonal fibres (figs. 22 and 23), which are set on end on the surface of the dentine, and fit into corresponding depressions in the same. They radiate in such a manner from the dentine that at the top of the tooth they are more or less vertical, while towards the sides they tend to the horizontal direction. Like the dentine-tubules, they are not straight, but disposed in wavy and parallel curves. The fibres are marked by transverse lines, and are mostly solid, but some of them contain a very minute canal.

Fig. 22.*

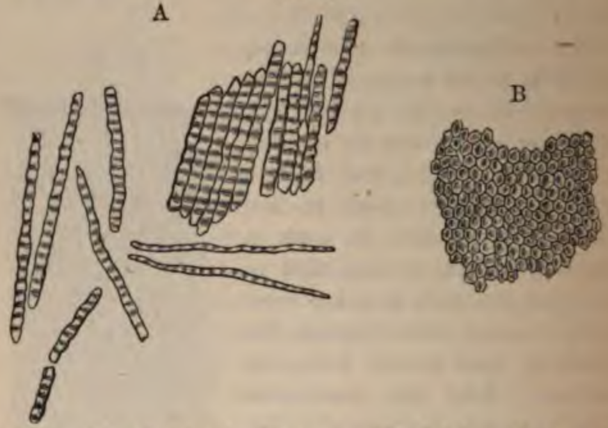
The enamel itself is coated on the outside by a very thin calcified membrane, sometimes termed the *cuticle* of the enamel.

The *crusta petrosa*, or *cement*, is composed of true bone, and in it are lacunæ and canaliculi which sometimes communicate with the outer finely-branched ends of the dentine-tubules.

* Fig. 22. Thin section of the enamel and a part of the dentine (from Kölliker) $\frac{350}{1}$. *a*, cuticular pellicle of the enamel; *b*, enamel fibres, or columns with fissures between them and cross striæ; *c*, larger cavities in the enamel, communicating with the extremities of some of the tubuli (*d*).

Development of Teeth.—The teeth are developed after the following manner:—Along the free edge of the toothless gum in the fœtus, there extends a groove, or small

Fig. 23*.



trench, the *primitive dental groove* (Goodsir), and, from the bottom of this, project ten small processes of mucous membrane, or *papillæ*, containing blood-vessels and nerves. As these *papillæ* grow up from below, the edges of the small trench begin to grow in towards each other, and overshadow them, at the same time that each papilla is cut off from its neighbour by the extension of a partition wall from the gum, which grows in from each side to separate the one from the other. Thus closed in above and all around, each dental papilla is at length contained in a separate sac, and gradually assumes the character of a tooth by deposition on its surface of the various hard matters which have been just enumerated as composing the greater part of a tooth's substance. The small vascular

* Fig. 23. Enamel fibres (from Kölliker) $\frac{350}{1}$. A, fragments and single fibres of the enamel, isolated by the action of hydrochloric acid. B, surface of a small fragment of enamel, showing the hexagonal ends of the fibres.

papilla is gradually encroached upon and imprisoned by the calcareous deposit, until only a small part of it is left as the *tooth-pulp,* which remains shut up in the harder substance, with only the before-mentioned small communication with the outside, through the end of the fang. In this manner the first set of teeth, or the *milk teeth,* are formed; and each tooth, by degrees developing, presses at length on the wall of the sac enclosing it, and causing its absorption, is *cut,* to use a familiar phrase.

The *temporary* or *milk teeth,* having only a very limited term of existence, gradually decay and are shed, while the *permanent* teeth push their way from beneath, by gradual increase and development, so as to succeed them.

The temporary teeth are ten in each jaw, namely, four *incisors,* two *canines,* and four *molars,* and are replaced by ten permanent teeth, each of which is developed from a small sac set by, so to speak, from the sac of the temporary tooth which precedes it, and called the *cavity of reserve.* The number of the permanent teeth is, however, increased to sixteen, by the development of three others on each side of the jaw after much the same fashion as that by which the milk teeth were themselves formed. The beginning of the development of the permanent teeth of course takes place long before the *cutting* of those which they are to succeed; one of the first acts of the newly-formed little dental sac of a milk-tooth being to set aside a portion of itself as the germ of its successor.

The following formula shows, at a glance, the comparative arrangement and number of the temporary and permanent teeth:—

		MO.	BI.	CA.	IN.	CA.	BI.	MO.		
Temporary Teeth .	Upper	2		1	4	1		2	=10	=20
	Lower	2		1	4	1		2	=10	
Permanent Teeth .	Upper	3	2	1	4	1	2	3	=16	=32
	Lower	3	2	1	4	1	2	3	=16	

From this formula it will be seen that the two bicuspid teeth in the adult are the successors of the two molars in the child. They differ from them, however, in some respects, the *temporary* molars having a stronger likeness to the *permanent* than to their immediate descendants, the so-called bicuspids. The temporary incisors and canines differ but little, except in their smaller size, from their successors.

CHAPTER V.

THE BLOOD.

Although it may seem, in some respects, unadvisable to describe the blood before entering upon the physiology of those subservient processes which have for their end or purpose its formation and development, yet there are many reasons for taking such a course, and we may therefore at once proceed to consider the structural and chemical composition of this fluid.

Wherever blood can be seen under a moderately high microscope-power as it flows in the vessels of a living part, it appears a colourless fluid containing minute coloured particles. The greater part of these particles are red, when seen *en masse*, and they are the source of the colour which, so far as the naked eye can see, belongs to every part of the blood alike. The colourless fluid is named *liquor sanguinis;* the particles are the *blood corpuscles* or *blood-cells*. The structural composition of the blood may be thus expressed:—

Liquid Blood	Corpuscles		Clot (containing also more or less serum.)
	Liquor Sanguinis or Plasma.	Fibrin	
		Serum	

When blood flows from the living body, it is a thickish heavy fluid, of a bright scarlet colour when it comes from an artery; deep purple, or nearly black, when it flows from

a vein. Its specific gravity at 60° F. is, on an average, 1055, that of water being reckoned as 1000; the extremes consistent with health being 1050 and 1059. Its temperature is generally about 100° F.; but it is not the same in all parts of the body. Thus, while the stream is slightly warmed by passing through the liver and some other parts, it is slightly cooled, according to Bernard, by traversing the capillaries of the skin. The temperature of blood in the left side of the heart is, again 1° or 2° higher than in the right (Savory).

The blood has a slight alkaline reaction; and emits an odour similar to that which issues from the skin or breath of the animal from which it flows, but fainter. The alkaline reaction appears to be a constant character of blood in all animals and under all circumstances. An exception has been supposed to exist in the case of menstrual blood; but the acid reaction which this sometimes presents is due to the mixture of an acid mucus from the uterus and vagina. Pure menstrual blood, such as may be obtained with a speculum, or from the uteri of women who die during menstruation, is always alkaline, and resembles ordinary blood. According to Bernard, blood becomes spontaneously acid after removal from the body, owing to conversion of its sugar into lactic acid.

The *odour* of blood is easily perceived in the watery vapour, or *halitus* as it is called, which rises from blood just drawn: it may also be set free, long afterwards, by adding to the blood a mixture of equal parts of sulphuric acid and water. It is said to be not difficult to tell, by the likeness of the odour to that of the body, the species of domestic animal from which any specimen of blood has been taken: the strong odour of the pig or cat, and the peculiar milky smell of the cow, are especially easy to be thus discerned in their blood (Barruel).

Quantity of Blood.

Only an imperfect indication of the whole quantity of blood in the body is afforded by measurement of that which escapes, when an animal is rapidly bled to death, inasmuch as a certain amount always remains in the blood vessels. In cases of less rapid bleeding, on the other hand, when life is more prolonged, and when, therefore, sufficient time elapses before death to allow some absorption into the circulating current of the fluids of the body (p. 84), the whole quantity of blood that escapes may be greater than the whole average amount naturally present in the vessels.

Various means have been devised, therefore, for obtaining a more accurate estimate than that which results from merely bleeding animals to death.

Welcker's method is the following. An animal is rapidly bled to death, and the blood which escapes is collected and measured. The blood remaining in the smaller vessels is then removed by the injection of water through them, and the mixture of blood and water thus obtained, is also collected. The animal is then finely minced, and infused in water, and the infusion is mixed with the combined blood and water previously obtained. Some of this fluid is then brushed on a white ground, and the colour compared with that of mixtures of blood and water whose proportions have been previously determined by measurement. In this way the materials are obtained for a fairly exact estimate of the quantity of blood actually existing in the body of the animal experimented on.

Another method (that of Vierordt) consists in estimating the amount of blood expelled from the ventricle, at each beat of the heart, and multiplying this quantity by the number of beats necessary for completing the 'round' of the circulation. This method is ingenious, but open to various objections, the most conclusive being the uncer-

tainty of all the premisses on which the conclusion is founded.

Other methods depend on the results of injecting a known quantity of water (Valentin) or of saline matters (Blake) into the blood-vessels; the calculation being founded in the first case, on the diminution of the specific gravity which ensues, and in the other, on the quantity of the salt found diffused in a certain measured amount of the blood abstracted for experiment.

A nearly correct estimate was probably made by Weber and Lehmann, from the following data. A criminal was weighed before and after decapitation; the difference in the weight representing, of course, the quantity of blood which escaped. The blood-vessels of the head and trunk, were then washed out by the injection of water, until the fluid which escaped had only a pale red or straw colour. This fluid was then also weighed; and the amount of blood which it represented was calculated, by comparing the proportion of solid matter contained in it, with that of the first blood which escaped on decapitation. Two experiments of this kind gave precisely similar results.

The most reliable of these various means for estimating the quantity of blood in the body yield as nearly similar results as can be expected, when the sources of error unavoidably present in all, are taken into consideration; and it may be stated that in man, the weight of the whole quantity of blood, compared with that of the body, is from about 1 to 8, to 1 to 10.

It must be remembered, however, that the whole quantity of blood varies, even in the same animal, very considerably, in correspondence with the different amounts of food and drink, which may have been recently taken in, and the equally varying quantity of matter given out. Bernard found by experiment, that the quantity of blood obtainable from a fasting animal is scarcely more than a half of that which is present soon after a full meal. The estimate above

given, must therefore be taken to represent only an approximate average.

Coagulation of the Blood.

When blood is drawn from the body, and left at rest, certain changes ensue, which constitute a kind of rough analysis of it, and are instructive respecting the nature of some of its constituents. After about ten minutes, taking a general average of many observations, it gradually clots or coagulates, becoming solid like a soft jelly. The clot thus formed has at first the same volume and appearance as the fluid blood had, and, like it, looks quite uniform; the only change seems to be, that the blood which was fluid is now solid. But presently, drops of transparent yellowish fluid begin to ooze from the surface of the solid clot; and these gradually collecting, first on its upper surface, and then all around it, the *clot* or "*crassamentum*," diminished in size, but firmer than it was before, floats in a quantity of yellowish fluid, which is named *serum*, the quantity of which may continually increase for from twenty-four to forty-eight hours after the clotting of the blood.

The changes just described may be thus explained. The *liquor sanguinis*, or liquid part of the blood (p. 56), consists of a thin fluid called serum, holding fibrin in solution.* The peculiar property of fibrin, as already said, is its tendency to become solid when at rest, and in some other conditions. When, therefore, a quantity of blood is drawn from the vessels, the fibrin coagulates, and the blood corpuscles, with part of the serum, are held, or, as it were, entangled in the solid substance which it forms.

But after healthy fibrin has thus coagulated, it always

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* This statement has been left unaltered in the text; but, as will be seen farther on, it requires modification.—(Ed.)

contracts; and what is generally described as one process of coagulation should rather be regarded as consisting of two parts or stages; namely, first, the simple act of clotting, coagulating, or becoming solid; and, secondly, the contraction or condensation of the solid clot thus formed. By this second act much of the serum which was soaked in the clot is gradually pressed out; and this collects in the vessel around the contracted clot.

Thus, by the observation of blood within the vessels, and of the changes which commonly ensue when it is drawn from them, we may distinguish in it three principal constituents, namely, 1*st*, the fibrin, or coagulating substance; 2*nd*, the serum; 3*rd*, the corpuscles.

That the fibrin is the only spontaneously coagulable material in the blood, may be proved in many ways; and most simply by employing any means whereby a portion of the liquor sanguinis, *i.e.*, the serum and fibrin, can be separated from the red corpuscles before coagulation. Under ordinary circumstances coagulation occurs before the red corpuscles have had time to subside; and thus, from their being entangled in the meshes of the fibrin, the clot is of a deep dark red colour throughout,—somewhat darker, it may be, at the most dependent part, from accumulation of red cells, but not to any very marked degree. If, however, from any cause, the red cells sink more quickly than usual, or the fibrin contracts more slowly, then, in either of these cases, the red corpuscles may be observed, while the blood is yet fluid, to sink below its surface; and the layer beneath which they have sunk, and which has usually an opaline or greyish white tint, will coagulate without them, and form a white clot consisting of fibrin alone, or of fibrin with entangled white corpuscles; for the white corpuscles, being very light, tend upwards towards the surface of the fluid. The layer of white clot which is thus formed rests on the top of a coloured clot of ordinary character, *i.e.*, of one in which

the coagulating fibrin has entangled the red corpuscles while they were sinking: and, thus placed, it constitutes what has been called a *buffy coat.*

When a buffy coat is formed in the manner just described, it commonly contracts more than the rest of the clot does, and, drawing in at its sides, produces a *cupped* appearance on the top of the clot.

In certain conditions of the system, and especially when there exists some local inflammation, this buffed and cupped condition of the clot is well marked, and there has been much discussion concerning its origin under these circumstances. It is now generally agreed that two causes combine to produce it.

In the first place, the tendency of the red corpuscles to form rouleaux (see p. 73) is much exaggerated in inflammatory blood; and as their rate of sinking increases with their aggregation, there is a ready explanation, at least in part, of the colourless condition of the top of the clot. And in the next place, inflammatory blood coagulates less rapidly than usual, and thus there is more time for the already rapidly sinking corpuscles to subside. The colourless or buffed condition of the upper part of the clot is therefore, readily accounted for; while the cupped appearance is easily explained by the greater power of contraction possessed by the fibrin of inflammatory blood, and by its contraction being now not interfered with by the presence of red corpuscles in its meshes.

Although the appearance just described is commonly the result of a condition of the blood in which there is an increase in the quantity of fibrin, it need not of necessity be so. For a very different state of the blood, such as that which exists in chlorosis, may give rise to the same appearance; but in this case the pale layer is due to a relatively smaller amount of red corpuscles, not to any increase in the quantity of fibrin.

It is thus evident that the coagulation of the blood is due

to its fibrin. The cause of the coagulation of the fibrin, however, is still a mystery.

The theory of Prof. Lister, that fibrin has no natural tendency to clot, but that its coagulation out of the body is due to the action of foreign matter with which it happens to be brought into contact, and, in the body, to conditions of the tissues, which cause them to act towards it like foreign matter, is insufficient; because even if it be true, it still leaves unexplained the manner in which the fibrin, fluid in the living blood-vessels, can, by foreign matter, be thus made solid. If it be a fact, it is a very important one, but it is not an explanation.

The same remark may be applied also to another theory which differs from the last, in that while it admits a natural tendency on the part of the blood to coagulation, it supposes that this tendency in the living body is restrained by some inhibitory power resident in the walls of the containing vessels. This also may, or may not, be true; but it is only a statement of a possible fact, and leaves unexplained the manner in which living tissue can thus restrain coagulation.

Dr. Draper believes that coagulation takes place in the living body, as out of it, or as in the dead; but in the one case the fibrin is picked out in the course of the circulation by tissues which this particular constituent of the blood is destined to nourish; in the others, it remains and becomes evident as a clot. This explanation is ingenious, but requires some kind of proof before it can be adopted.

Concerning other theories, as for instance, that coagulation is due to the escape of carbonic acid, or of ammonia, it need only be said that they have been completely disproved.

We must therefore, for the present, believe that the cause of the coagulation of the blood has yet to be dis-

covered; but some very interesting observations in connexion with the subject have been recently made, and seem not unlikely to lead in time to a solution of this difficult and most vexed question. The observations referred to have been made independently by Alexander Schmidt, although he was forestalled in regard to some of his experiments by Dr. Andrew Buchanan of Glasgow, many years ago.

When blood-serum, or washed blood-clot, is added to the fluid of hydrocele, or any other serous effusion, it speedily causes coagulation, and the production of true fibrin. And this phenomenon occurs also on the admixture of serous effusions from different parts of the body, as that of hydrocele with that of ascites, or of either with fluid from the cavity of the pleura. Other substances also, as muscular or nervous tissue, skin, etc., have been found also able to excite coagulation in serous fluids. Thus, fluids which have little or no tendency to coagulate when left to themselves, can be made to produce a clot, apparently identical with the fibrin of blood by the addition to them of matter which, on its part, was not known to have any special relation to fibrin. As may be supposed, the coagulation is not alike in extent under all these circumstances. Thus, although it occurs when apparently few or no blood-cells exist in either constituent of the mixture, yet the addition of these very much increases the effect, and their presence evidently has a very close connexion with the process. From the action of the buffy coat of a clot, in causing the appearance of fibrin in serous effusions, it may be inferred that the pale as well as the red corpuscles are influential in coagulation under these circumstances. Blood-crystals are also found to be effective in producing a clot in serous fluids.

The true explanation of these very curious phenomena is, probably, not fully known; but Schmidt supposes that in the act of formation of fibrin there occurs the union

of two substances, which he terms fibrino-plastin and fibrinogen.

The substance which he terms fibrino-plastin, and which he has obtained, not only from blood, but from many other liquids and solids, as the crystalline lens, chyle and lymph, connective tissue, etc., which are found capable of exciting coagulation in serous fluids, is probably identical with the globulin of the red corpuscles.

The fibrinogenous matter obtained from serous effusions differs but little, chemically, from the fibrino-plastin.

Thus in the experiment before mentioned, the globulin or fibrino-plastic matter of the blood-cells in the clot, causes coagulation by uniting with the fibrinogen present in the hydrocele-fluid. And whenever there occurs coagulation with the production of fibrin, whether in ordinary blood-clotting, or in the admixture of serous effusions, or in any other way, a like union of these two substances may be supposed to occur.

The main result, therefore, of these very interesting experiments and observations has been to make it probable that the idea of fibrin existing in a liquid state in the blood is founded on a mistaken notion of its real nature, and that, probably, it does not exist at all in solution as fibrin, but is formed at the moment of coagulation by the union of two substances which, in fluid blood, exist separately.

The theories before referred to, concerning the coagulation of the blood, will therefore, if this be true, resolve themselves into theories concerning the causes of the union of fibrino-plastin and fibrinogen; and whether, on the one hand, it is an inhibitory action of the living blood-vessels that naturally *restrains*, or a catalytic action of foreign matter that *excites*, the union of these two substances.

Conditions affecting Coagulation.

Although the coagulation of fibrin appears to be spontaneous, yet it is liable to be modified by the conditions in which it is placed; such as temperature, motion, the access of air, the substances with which it is in contact, the mode of death, etc. All these conditions need to be considered in the study of the coagulation of the blood.

The coagulation of the blood is hastened by the following means :—

1. Moderate warmth,—from about 100° F. to 120° F.

2. *Rest* is favourable to the coagulation of blood. Blood, of which the whole mass is kept in uniform motion, as when a closed vessel completely filled with it is constantly moved, coagulates very slowly and imperfectly. But rest is not essential to coagulation; for the coagulated fibrin may be quickly obtained from blood by stirring it with a bundle of small twigs; and whenever any rough points of earthy matter or foreign bodies are introduced into the blood-vessels, the blood soon coagulates upon them.

3. Contact with foreign matter, and especially multiplication of the points of contact. Thus, when all other conditions are unfavourable, the blood will coagulate upon rough bodies projecting into the vessels; as, for example, upon threads passed through arteries or aneurismal sacs, or the heart's valves roughened by inflammatory deposits or calcareous accumulations. And, perhaps, this may explain the quicker coagulation of blood after death in the heart with walls made irregular by the fleshy columns, than in the simple smooth walled arteries and veins.

4. The free access of air.

5. Coagulation is quicker in shallow, than in tall and narrow vessels.

6. The addition of less than twice the bulk of water.

The blood last drawn is said to coagulate more quickly than that which is first let out.

The coagulation of the blood is retarded by the following means:—

1. *Cold* retards the coagulation of blood; and it is said that, so long as blood is kept at a temperature below 40° F., it will not coagulate at all. Freezing the blood, of course, prevents its coagulation; yet it will coagulate, though not firmly, if thawed after being frozen; and it will do so, even after it has been frozen for several months. Coagulation is accelerated, but the subsequent contraction of the clot is hindered, by a temperature between 100° and 120°: a higher temperature retards coagulation, or, by coagulating the albumen of the serum, prevents it altogether.

2. The addition of water in greater proportion than twice the bulk of the blood.

3. Contact with living tissues, and especially with the interior of a living blood-vessel, retards coagulation, although if the blood be at rest it does not prevent it.

4. The addition of the alkaline and earthy salts in the proportion of 2 or 3 per cent. and upwards. When added in large proportion most of these saline substances prevent coagulation altogether. Coagulation, however, ensues on dilution with water. The time that blood can be thus preserved in a liquid state and coagulated by the addition of water, is quite indefinite.

5. Imperfect aëration,—as in the blood of those who die by asphyxia.

6. In inflammatory states of the system, the blood coagulates more slowly although more firmly.

7. Coagulation is retarded by exclusion of the blood from the air, as by pouring oil on the surface, etc. In vacuo, the blood coagulates quickly; but Prof. Lister thinks that the rapidity of the process is due to the bubbling which ensues from the escape of gas, and to the blood being thus brought more freely into contact with the containing vessel.

The coagulation of the blood is prevented altogether by the addition of strong acids and caustic alkalies.

It has been believed, and chiefly on the authority of Mr. Hunter, that, after certain modes of death, the blood does not coagulate; he enumerates the death by lightning, over-exertion (as in animals hunted to death), blows on the stomach, fits of anger. He says, "I have seen instances of them all." Doubtless he had done so; but the results of such events are not constant. The blood has been often observed coagulated in the bodies of animals killed by lightning or an electric shock; and Mr. Gulliver has published instances in which he found clots in the hearts of hares and stags hunted to death, and of cocks killed in fighting.

Chemical Composition of the Blood.

Among the many analyses of the blood that have been published, some, in which all the constituents are enumerated, are inaccurate in their statements of the proportions of those constituents; others, admirably accurate in some particulars, are incomplete. The two following tables, constructed chiefly from the analyses of Denis, Lecanu, Simon, Nasse, Lehmann, Becquerel, Rodier, and Gavarret, are designed to combine, as far as possible, the advantage of accuracy in numbers with the convenience of presenting at one view, a list of all the constituents of the blood.

Average proportions of the principal constituents of the blood in 1,000 parts:—

Water	784·
Red corpuscles (solid residue)	130·
Albumen of serum	70·
Saline matters	6·03
Extractive, fatty, and other matters	7·77
Fibrin	2·2
	1000

Average proportions of all the constituents of the blood in 1,000 parts:—

Water		784·
Albumen		70·
Fibrin		2·2
Red corpuscles (dry)		130·
Fatty Matters		1·4
Inorganic Salts:	Chloride of sodium	3·6
	Chloride of potassium	0·35
	Tribasic phosphate of soda	0·2
	Carbonate of soda	0·28
	Sulphate of soda	0·28
	Phosphates of lime and magnesia	0·25
	Oxide and Phosphate of iron	0·5
Extractive matters, biliary colouring matter, gases, and accidental substances		6·40
		1000·

Elementary composition of the dried blood of the ox:—

Carbon	57·9
Hydrogen	7·1
Nitrogen	17·4
Oxygen	19·2
Ashes	4·4

These results of the ultimate analysis of ox's blood afford a remarkable illustration of its general purpose, as supplying the materials for the renovation of all the tissues. For the analysts (Playfair and Boeckmann) have found that the flesh of the ox yields the same elements in so nearly the same proportions, that the elementary composition of the organic constituents of the blood and flesh may be considered identical, and may be represented for both by the formula $C_{45}H_{39}N_6O_{15}$.

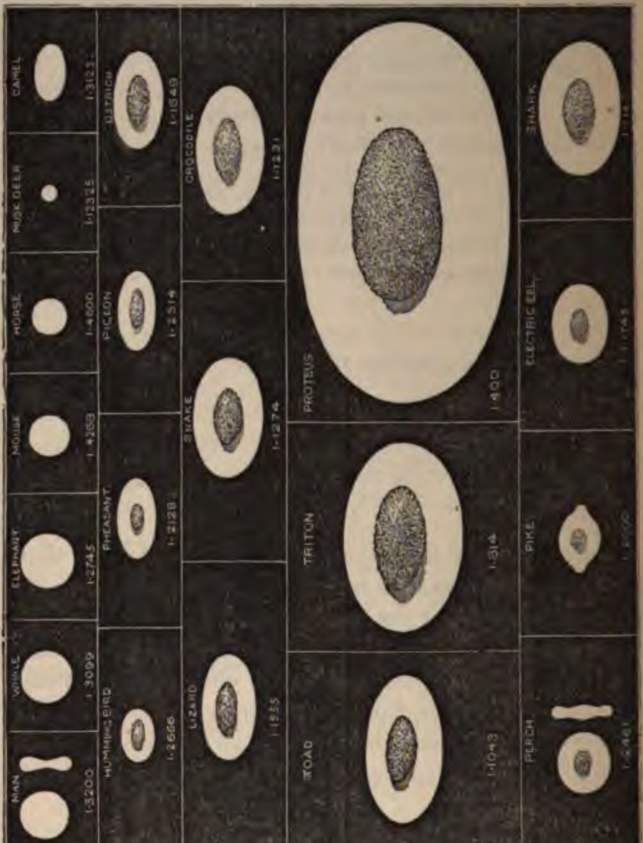
The Blood-Corpuscles or Blood-Cells.

It has been already said, that the clot of blood contains, with the fibrin and the portion of the serum that is soaked in it, the *blood-corpuscles*, or *blood-cells*. Of these there are

two principal forms, the red and the white corpuscles. When coagulation has taken place quickly, both kinds of

Fig. 24.*

Mammals. Birds. Reptiles. Amphibia. Fish.



* The above illustration is somewhat altered from a drawing, by Mr. Gulliver, in the Proceed. Zool. Society, and exhibits the typical characters of the red blood-cells in the main divisions of the Vertebrata. The fractions are those of an inch, and represent the average diameter. In

corpuscles may be uniformly diffused through the clot; but, when it has been slow, the red corpuscles, being the heaviest constituent of the blood, tend by gravitation to accumulate at the bottom of the clot; and the white corpuscles, being among the lightest constituents, collect in the upper part, and contribute to the formation of the buffy coat.

The *human red blood-cells* or *blood-corpuscles* (figs. 25 and 29) are circular flattened disks of different sizes, the majority varying in diameter from $\frac{1}{3000}$ to $\frac{1}{4000}$ of an inch, and about $\frac{1}{10000}$ of an inch in thickness. When viewed singly, they appear of a pale yellowish tinge; the deep red colour which they give to the blood being observable in them only when they are seen *en masse*. Their borders are rounded; their surfaces, in the perfect and most usual state, slightly concave; but they readily acquire flat or convex surfaces when, the liquor sanguinis being diluted, they are swollen by absorption of fluid. They are composed of a colourless, structureless, and transparent filmy framework or *stroma*, infiltrated in all parts by a red colouring-matter termed *hæmoglobin*. The *stroma* is tough and elastic, so that, as the cells circulate, they admit of elongation and other changes of form, in adaptation to the vessels, yet recover their natural shape as soon as they escape from compression. The term cell, in the sense of a bag or sac, is inapplicable to the red blood-corpuscle; and it must be con-

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the case of the oval cells, only the long diameter is here given. It is remarkable, that although the size of the red blood-cells varies so much in the different classes of the vertebrate kingdom, that of the white corpuscles remains comparatively uniform, and thus they are, in some animals, much greater, in others much less than the red corpuscles existing side by side with them.

It may be here remarked, that the appearance of a nucleus in the red blood-cells of birds, reptiles, amphibia and fish, has been shown by Mr. Savory to be the result of post-mortem change; no nucleus being visible in the cells as they circulate in the living body, or in those which have just escaped from the blood-vessels.

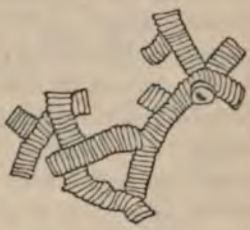
sidered, if not solid throughout, yet as having no such variety of consistence in different parts as to justify the notion of its being a membranous sac with fluid contents. The stroma exists in all parts of its substance, and the colouring-matter uniformly pervades this, and is not merely surrounded by and mechanically enclosed within the outer wall of the corpuscle. The red corpuscles have no nuclei, although, in their usual state, the unequal refraction of transmitted light gives the appearance of a central spot, brighter or darker than the border, according as it is viewed in or out of focus. Their specific gravity is about 1088.

In examining a number of red corpuscles with the microscope, it is easy to observe certain natural diversities among them, though they may have been all taken from the same part. The great majority, indeed, are very uniform; but some are rather larger, and the larger ones generally appear paler and less exactly circular than the rest; their surfaces also are, usually, flat or slightly convex, they often contain a minute shining particle like a nucleolus, and they are lighter than the rest, floating higher in the fluid in which they are placed. Other deviations from the general characters assigned to the corpuscles, depend on changes that occur after they are taken from the body. Very commonly they assume a granulated or mulberry-like form, in consequence, apparently, of a peculiar corrugation of their cell-walls. Sometimes, from the same cause, they present a very irregular, jagged, indented, or star-like appearance. The larger cells are much less liable to this change than the smaller, and the natural shape may be restored by diluting the fluid in which the corpuscles float; by such dilution the corpuscles, as already said, may be made to swell up, by absorbing the fluid; and, if much water be added, they will become spherical and pellucid, their colouring matter being dissolved, and, as it were, washed out of them. Some of them may thus be burst; the others

are made obscure; but many of these latter may be brought into view again by evaporating, or adding saline matter to, the fluid, so as to restore it to its previous density. The changes thus produced by water are more quickly effected by weak acetic acid, which immediately makes the corpuscles pellucid, but dissolves few or none of them, for the addition of an alkali, so as to neutralize the acid, will restore their form though not their colour.

A peculiar property of the red corpuscles, which is exaggerated in inflammatory blood, and which appears to exist in a marked degree in the blood of horses, may be here noticed. It gives them a great tendency to adhere together in rolls or columns, like piles of coins, and then, very quickly, these rolls fasten together by their ends, and cluster; so that, when the blood is spread out thinly on a glass, they form a kind of irregular network, with crowds of corpuscles at the several points corresponding with the knots of the net (fig. 25). Hence, the clot formed in such a thin layer of blood looks mottled with blotches of pink upon a white ground: in a larger quantity of such blood, as soon as the corpuscles have clustered and collected in rolls (that is, generally in two or three minutes after the blood is drawn), they begin to sink very quickly; for in the aggregate they present less surface to the resistance of the liquor sanguinis than they would if sinking separately. Thus quickly sinking, they leave above them a layer of liquor sanguinis, and this coagulating, forms a buffy coat, as before described, the volume of which is augmented by the white corpuscles, which have no tendency to adhere to the red ones, and by their lightness float up clear of them.

*Fig. 25.**



* Fig. 25. Red corpuscles collected into rolls (after Henle.)

Chemical Composition of Red Blood-cells.

It has been before remarked that the red blood-corpuscles are formed of a colourless *stroma*, infiltrated with a colouring matter termed *hæmoglobin*. As they exist in the blood they contain about three-fourths of their weight of water.

The stroma appears to be composed of a nitrogenous proximate principle termed *protagon*, combined with albuminous matter (paraglobulin or fibrinoplastin), fatty matters including cholesterin, and salts, chiefly phosphates, of potash, soda and lime.

Hæmoglobin, which enters far more largely into the composition of the red corpuscles than any other of their constituents, is allied to albumen in some respects, but differs remarkably from it in others. One of its most marked distinctive characters is its tendency under certain artificial conditions to crystallize; the so-called *blood-crystals* being but the natural crystalline forms assumed by this substance.

Hæmoglobin can be obtained in a crystalline form with various degrees of difficulty from the blood of different animals, that of man holding an intermediate place in this respect. Among the animals whose blood colouring-matter crystallizes most readily are the guinea-pig and the dog; and in these cases to obtain crystals it is generally sufficient to dilute a drop of recently drawn blood with water and expose it for a few minutes to the air. In many instances, however, a somewhat less simple process must be adopted; as the addition of chloroform or ether, rapid freezing and then thawing, or other means which separate the colouring-matter from the other constituents of the corpuscles.

Different forms of blood-crystals are shown in the accompanying figures.

Another and most important character of hæmoglobin is its attraction for oxygen, and some other gases, as carbonic

and nitrous oxides, with all of which it appears to form definite chemical combinations. The combination with oxygen is that which is of most physiological importance. During the passage of the blood through the lungs, it is constantly formed; while it is as constantly decomposed, in consequence of the readiness with which hæmoglobin parts with oxygen, when the latter is exposed to other attractions in its circulation through the systemic capillaries. Thus, the red corpuscles, in virtue of their colouring matter, which readily absorbs oxygen and as readily gives it up again, are the chief means by which oxygen is carried in the blood (see also p. 85).

*Fig. 26.**

Fig. 27.†

* Figs. 26, 27, and 28, illustrate some of the principal forms of blood-crystals :—

Fig. 26, Prismatic, from human blood.

† Fig. 27, Tetrahedral, from blood of the guinea-pig.

By heat, mineral and other acids, alkalies, &c., hæmoglobin is decomposed into an albuminous matter (resembling globulin) and *hæmatin*. The latter, now known to be a product of the decomposition of hæmoglobin, was once thought to be the natural colouring matter of the blood.

Fig. 28*.

The White Corpuscles of the Blood or Blood Leucocytes.

The *white* corpuscles are much less numerous than the *red*. On an average, in health, there may be one white to 400 or 500 red corpuscles; but in disease, the proportion is often as high as one to ten, and sometimes even much higher.

In health, the proportion varies considerably even in the course of the same day. The variations appear to depend chiefly on the amount and probably also on the kind of food taken; the number of leucocytes being very considerably increased by a meal, and diminished again on fasting.

They present greater diversities of form than the red ones do; but the gradations between the extreme forms are so regular, that no sufficient reason can be found for supposing that there is in healthy blood more than one species of white corpuscles. In their most general appear-

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* Fig. 28. Hexagonal crystals, from blood of squirrel. On these six-sided plates, prismatic crystals, grouped in a stellate manner, not unfrequently occur (after Funke).

ance, they are circular and nearly spherical, about $\frac{1}{2500}$ of an inch in diameter (fig. 29). They have a greyish, pearly look, appearing variously shaded or nebulous, the shading being much darker in some than in others. They seem to be formed of protoplasm (p. 19), containing granules which are in some specimens few and very distinct, in others (though rarely) so numerous that the whole corpuscle looks like a mass of granules.

*Fig. 29.**

These corpuscles cannot be said to have any true cell-wall. In a few instances an apparent cell-membrane can be traced around them; but, much more commonly, even this is not discernible till after the addition of water or dilute acetic acid, which penetrates the corpuscle, and lifts up and distends what looks like a cell-wall, to the interior of which the material, that before appeared to form the whole corpuscle, remains attached as the nucleus of the cell (fig. 29).

A remarkable property of the white corpuscles, first observed by Mr. Wharton Jones, consists in their capability of assuming different forms, irrespective of any external influence. If a drop of blood be examined with a high microscope power under conditions by which loss of moisture is prevented, at the same time that the temperature is maintained at about the degree natural to the blood as it circulates in the living body, the leu-

* Fig. 29. Red and white blood-corpuscles. *a*, White corpuscle of natural aspect: *b*, Three white corpuscles acted on by weak acetic acid. *c*, Red blood-corpuscles.

cocytes can be seen alternately contracting and dilating very slowly at various parts of their circumference,—shooting out irregular processes, and again withdrawing them partially or completely, and thus in succession assuming various irregular forms.

These movements, called *amœboid*, from their resemblance to the movements exhibited by an animal called the *Amœba*, the structure of which is as simple as that of a white blood-corpuscle, are characteristic of the living leucocyte, and form a good example of the contractile property of protoplasm, before referred to. Indeed, the unchanging rounded form which the corpuscles present in specimens of blood examined in the ordinary manner under the microscope, must be looked upon as the shape natural to a dead corpuscle, or one whose vitality is dormant, rather than as the proper shape of one living and active.

Besides the red and white corpuscles, the microscope reveals numerous minute *molecules* or *granules* in the blood, circular or spherical, and varying in size from the most minute visible speck to the $\frac{1}{8000}$ of an inch (Gulliver). These molecules are very similar to those found in the lymph and chyle, and are, some of them, fatty, being soluble in ether, others probably albuminous, being soluble in acetic acid. Generally, also, there may be detected in the blood, especially during the height of digestion, very minute equal-sized fatty particles, similar to those of which the molecular base of chyle is constituted (Gulliver).

The Serum.

The *serum* is the liquid part of the blood remaining after the coagulation of the fibrine. In the usual mode of coagulation, part of the serum remains soaked in the clot, and the rest, squeezed from the clot by its contraction, lies around and over it. The quantity of serum that appears around the clot depends partly on the total quantity in the blood, but partly also on the degree to which the clot con-

tracts. This is affected by many circumstances: generally, the faster the coagulation the less is the amount of contraction; and, therefore, when blood coagulates quickly, it will appear to contain a small proportion of serum. Hence, the serum always appears deficient in blood drawn slowly into a shallow vessel, abundant in inflammatory blood drawn into a tall vessel. In all cases, too, it should be remembered, that, since the contraction of the clot may continue for thirty-six or more hours, the quantity of serum in the blood cannot be even roughly estimated till this period has elapsed.

The serum is an alkaline, slimy or viscid, yellowish fluid, often presenting a slight greenish, or greyish hue, and with a specific gravity of from 1025 to 1030. It is composed of a mixture of various substances dissolved in about nine times their weight of water. It contains, indeed, the greater part of all the substances enumerated as existing in the blood, with the exception of the fibrin and the red corpuscles. Its principal constituent is albumen, of which it contains about 8 per cent., and the coagulation of which, when heated, converts nearly the whole of the serum into a solid mass. The liquid which remains uncoagulated, and which is often enclosed in little cavities in the coagulated serum, is called *serosity*: it contains, dissolved in water, fatty, extractive, and saline matters.

Variations in the principal Constituents of the Liquor Sanguinis.

The *water of the blood* is subject to hourly variations in its quantity, according to the period since the taking of food, the amount of bodily exercise, the state of the atmosphere, and all the other events that may affect either the ingestion or the excretion of fluids. According to these conditions, it may vary from 700 to 790 parts in the thousand. Yet uniformity is on the whole maintained; because nearly all those things which tend to lower the proportion of water in the blood, such as active exercise, or the addition of saline and other solid matter, excite thirst; while, on the

other hand, the addition of an excess of water to the blood is quickly followed by its more copious excretion in sweat and urine. And these means for adjusting the proportion of the water find their purpose in maintaining certain important physical conditions in the blood; such as its proper viscidity, and the degree of its adhesion to the vessels through which it ought to flow with the least possible resistance from friction. On this also depends, in great measure, the activity of absorption by the blood-vessels, into which no fluids will quickly penetrate, but such as are of less density than the blood. Again, the quantity of water in the blood determines chiefly its volume, and thereby the fulness and tension of the vessels and the quantity of fluid that will exude from them to keep the tissues moist. Finally, the water is the general solvent of all the other materials of the liquor sanguinis.

It is remarkable, that the proportion of water in the blood may be sometimes increased even during its abstraction from an artery or vein. Thus Dr. Zimmerman in bleeding dogs, found the last drawn portion of blood contain 12 or 13 parts more of water in 1000 than the blood first drawn; and Polli noticed a corresponding diminution in the specific gravity of the human blood during venesection, and suggested the only probable explanation of the fact, namely, that during bleeding, the blood-vessels absorb very quickly a part of the serous fluid with which all the tissues are moistened.

The *albumen* may vary, consistently with health, from 60 to 70 parts in the 1000 of blood. The form in which it exists in the blood is not yet certain. It may be that of simple solution as pure albumen: but it is, more probably, in combination with soda, as an albuminate of soda; for, if serum be much diluted with water, and then neutralized with acetic acid, pure albumen is deposited. Another view entertained by Enderlin is that the albumen is dissolved in the solution of the neutral phosphate of sodium,

to which he considers the alkaline reaction of the blood to be due, and solutions of which can dissolve large quantities of albumen and phosphate of lime.

The proportion of *fibrin* in healthy blood may vary between 2 and 3 parts in 1000. In some diseases, such as typhus, and others of low type, it may be as little as 1·034; in other diseases, it is said, it may be increased to as much as 7·528 parts in 1000. But, in estimating the quantity of fibrin, chemists have not taken account of the white corpuscles of the blood. These cannot, by any mode of analysis yet invented, be separated from the fibrin of mammalian blood: their composition is unknown, but their weight is always included in the estimate of the fibrin. In health, they may, perhaps, add too little to its weight to merit consideration, but in many diseases, especially in inflammatory and other blood diseases in which the fibrin is said to be increased, these corpuscles become so numerous that a large proportion of the supposed increase of the fibrin must be due to their being weighed with it. On this account all the statements respecting the increase of fibrin in certain diseases need revision.

The enumeration of the *fatty matters* of the blood makes it probable that most of those which are found in the tissues or secretions exist also ready-formed in the blood; for it contains the cholesterin of the bile, the cerebrin and phosphorised fat of the brain, and the ordinary saponifiable fats, stearin, olein, and palmitin. A volatile fatty acid is that on which the odour of the blood mainly depends; and it is supposed that when sulphuric acid is added (see p. 57), it evolves the odour by combining with the base with which, naturally, this acid is neutralized. According to Lehmann, much of the fatty matter of the blood is accumulated in the red corpuscles.

These fatty matters are subject to much variation in quantity, being commonly increased after every meal in which fat, or starch, or saccharine substances have been

taken. At such times, the fatty particles of the chyle, added quickly to the blood, are only gradually assimilated; and their quantity may be sufficient to make the serum of the blood opaque, or even milk-like.

As regards the *inorganic constituents* of the blood,—the substances which remain as *ashes* after its complete burning —one may observe in general their small quantity in proportion to that of the animal matter contained in it. Those among them of peculiar interest are the phosphate and carbonate of sodium, and the phosphate of calcium. It appears most probable, that the blood owes its alkaline reaction to both these salts of sodium. The existence of the neutral phosphate ($Na_2H.PO_4$) was proved by Enderlin: the presence of carbonate of sodium has been proved by Lehmann and others.

In illustration of the characters which the blood may derive from the phosphate of sodium, Liebig points out the large capacity which solutions of that salt have of absorbing carbonic acid gas, and then very readily giving it off again when agitated in atmospheric air, and when the atmospheric pressure is diminished. It is probably, also, by means of this salt, that the phosphate of calcium is held in solution in the blood in a form in which it is not soluble in water, or in a solution of albumen. Of the remaining inorganic constituents of the blood, the oxide and phosphate of iron referred to, exist in the liquor sanguinis, independently of the iron in the corpuscles.

Schmidt's investigations have shown that the inorganic constituents of the blood-cells somewhat differ from those contained in the serum; the former possessing a considerable preponderance of phosphates and of the salts of potassium, while the chlorides, especially of sodium, with phosphate of sodium, are particularly abundant in the latter.

Among the *extractive matters* of the blood, the most noteworthy are *Creatin* and *Creatinin*. Besides these, other organic principles have been found either constantly

or generally in the blood, including *casein*, especially in women during lactation: *glucose*, or *grape-sugar*, found in the blood of the hepatic vein, but disappearing during its transit through the lungs (Bernard); *urea*, and in very minute quantities, *uric acid* (Garrod); *hippuric* and *lactic acids*; *ammonia* (Richardson): and lastly, certain *colouring* and *odoriferous* matters.

Variations in healthy Blood under different Circumstances.

As the general condition of the body depends so much on the condition of the blood, and as, on the other hand, anything that affects the body must sooner or later, and to a greater or less degree, affect the blood also, it might be expected that considerable variations in the qualities of this fluid would be found under different circumstances of disease; and such is found to be the case. Even in health, however, the general composition of the blood varies considerably.

The conditions which appear most to influence the composition of the blood in health, are these: sex, pregnancy, age, and temperament. The composition of the blood is also, of course, much influenced by diet.

1. *Sex.*—The blood of men differs from that of women, chiefly in being of somewhat higher specific gravity, from its containing a relatively larger quantity of red corpuscles.

2. *Pregnancy.*—The blood of pregnant women has a rather lower specific gravity than the average, from deficiency of red corpuscles. The quantity of white corpuscles, on the other hand, and of fibrin, is increased.

3. *Age.*—From the analysis of Denis it appears that the blood of the fœtus is very rich in solid matter, and especially in red corpuscles; and this condition, gradually diminishing, continues for some weeks after birth. The quantity of solid matter then falls during childhood below the average, again rises during adult life, and in old age falls again.

4. *Temperament.*—But little more is known concerning the connection of this with the condition of the blood, than that there appears to be a relatively larger quantity of solid matter, and particularly of red corpuscles, in those of a plethoric or sanguineous temperament.

5. *Diet.*—Such differences in the composition of the blood as are due to the temporary presence of various matters absorbed with the food and drink, as well as the more lasting changes which must result from generous or poor diet respectively, need be here only referred to.

Effects of Bleeding.—The result of bleeding is to diminish the specific gravity of the blood; and so quickly, that in a single venesection, the portion of blood last drawn has often a less specific gravity than that of the blood that flowed first (J. Davy and Polli). This is, of course, due to absorption of fluid from the tissues of the body. The physiological import of this fact, namely, the instant absorption of liquid from the tissues, is the same as that of the intense thirst which is so common after either loss of blood, or the abstraction from it of watery fluid, as in cholera, diabetes, and the like.

For some little time after bleeding, the want of red blood-cells is well marked; but with this exception, no considerable alteration seems to be produced in the composition of the blood for more than a very short time, the loss of the other constituents, including the pale corpuscles, being very quickly repaired.

Variations in the Composition of the Blood, in different Parts of the Body.

The composition of the blood, as might be expected, is found to vary in different parts of the body. Thus arterial blood differs from venous; and although its composition and general characters are uniform throughout the whole course of the systemic arteries, they are not so throughout

the venous system,—the blood contained in some veins differing remarkably from that in others.

1. *Differences between arterial and venous blood.*—These may be arranged under two heads,—differences in *colour*, and in *general composition.*

a. Colour.—Concerning the cause of the difference in colour between arterial and venous blood, there has been much doubt, not to say confusion. For while the scarlet colour of the arterial blood has been supposed by some observers, and for some reasons, to be due to the chemical action of oxygen, and the purple tint of that in the veins to the action of carbonic acid, there are facts which made it seem probable that the cause was a mechanical one rather than a chemical, and that it depended on a difference in the shape of the red corpuscles, by which their power of transmitting and reflecting light was altered. Thus, carbonic acid was thought to make the blood dark by causing the red cells to assume a bi-convex outline, and oxygen was supposed to reverse the effect by contracting them and rendering them bi-concave. We may believe, however, that, at least for the present, this vexed question has, by the results of investigations undertaken by Professor Stokes and others, been now set at rest.

The colouring matter of the blood, or hæmoglobin (p. 74), is capable of existing in two different states of oxidation, and the respective colours of arterial and venous blood are caused by differences in tint between these two varieties—oxidised or scarlet hæmoglobin and deoxidised or purple hæmoglobin. The change of colour produced by the passage of the blood through the lungs, and its consequent exposure to oxygen, is due, probably, to the oxidation of purple, and its conversion into scarlet hæmoglobin; while the readiness with which the latter is de-oxidised offers a reasonable explanation of the change, in regard to tint, of arterial into venous blood,—the transformation being effected by the delivering up of oxygen to the tissues, by

the scarlet hæmoglobin, during the blood's passage through the capillaries. The changes of colour are more probably due to this cause, namely, a varying quantity of oxygen chemically combined with the hæmoglobin, than to any mechanical effect of this gas, or to the influence of carbonic acid, either chemically, on the colouring matter, or mechanically, on the corpuscles which contain it. We are not, perhaps, in a position to deny altogether the possible influence of mechanical conditions of the red corpuscles on the colour of arterial and venous blood respectively; but it is probable that this cause alone would be quite insufficient to explain the differences in the colour of the two kinds of blood, and therefore if it be an element at all in the change, it must be allowed to take only a subordinate position.

The distinction between the two kinds of hæmoglobin naturally present in the blood, or in other words, the proof that the addition or subtraction of oxygen involves the production respectively of two substances having fundamental differences of chemical constitution, has been made out chiefly by *spectrum-analysis*,—the effects produced by placing oxidised and de-oxidised solutions of hæmoglobin in the path of a ray of light traversing a spectroscope being different. For while the oxidised solution causes the appearance of two absorption bands in the yellow and the green part of the *spectrum*, these are replaced by a single band intermediate in position, when the oxidised or scarlet solution is darkened by de-oxidising agencies,—or, in other words, when the change which naturally ensues in the conversion of arterial into venous blood is artificially produced.*

The greater part of the hæmoglobin in both arterial and venous blood probably exists in the scarlet or more highly oxidised condition, and only a small part is de-oxidised and made purple in its passage from the arteries into the veins.

* The student to whom the terms employed in connection with spectrum-analysis are not familiar, is advised to consult, with reference to the preceding paragraph, an elementary treatise on Physics.

The differences in regard to colour between arterial and venous blood are sometimes not to be observed. If blood runs very slowly from an artery, as from the bottom of a deep and devious wound, it is often as dark as venous blood. In persons nearly asphyxiated also, and sometimes, under the influence of chloroform or ether, the arterial blood becomes like the venous. In the fœtus also both kinds of blood are dark. But, in all these cases, the dark blood becomes bright on exposure to the air. Bernard has shown that venous blood returning from a gland in active secretion is almost as bright as arterial blood.

b. General Composition.—The chief differences between arterial and ordinary venous blood are these. Arterial blood contains rather more fibrin, and rather less albumen and fat. It coagulates somewhat more quickly. Also, it contains more oxygen, and less carbonic acid. According to Denis, the fibrin of venous blood differs from arterial, in that when it is fresh and has not been much exposed to the air, it may be dissolved in a slightly heated solution of nitrate of potassium.

Some of the veins, however, contain blood which differs from the ordinary standard considerably. These are the portal, the hepatic, and the splenic veins.

Portal vein.—The blood which the portal vein conveys to the liver is supplied from two chief sources; namely, that in the gastric and mesenteric veins, which contains the soluble elements of food absorbed from the stomach and intestines during digestion, and that in the splenic vein; it must, therefore, combine the qualities of the blood from each of these sources.

The blood in the gastric and mesenteric veins will vary much according to the stage of digestion and the nature of the food taken, and can therefore be seldom exactly the same. Speaking generally, and without considering the sugar, dextrine, and other soluble matters which may have been absorbed from the alimentary canal, this blood

appears to be deficient in solid matters, especially in red corpuscles, owing to dilution by the quantity of water absorbed, to contain an excess of albumen, though chiefly of a lower kind than usual, resulting from the digestion of nitrogenised substances, and termed albuminose, and to yield a less tenacious kind of fibrin than that of blood generally.

The blood from the splenic vein is probably more definite in composition, though also liable to alterations according to the stage of the digestive process, and other circumstances. It seems generally to be deficient in red corpuscles, and to contain an unusually large proportion of albumen. The fibrin seems to vary in relative amount, but to be almost always above the average. The proportion of colourless corpuscles appears also to be unusually large. The whole quantity of solid matter is decreased, the diminution appearing to be chiefly in the proportion of red corpuscles.

The blood of the portal vein, combining the peculiarities of its two factors, the splenic and mesenteric venous blood, is usually of lower specific gravity than blood generally, is more watery, contains fewer red corpuscles, more albumen, chiefly in the form of albuminose, and yields a less firm clot than that yielded by other blood, owing to the deficient tenacity of its fibrin. These characteristics of portal blood refer to the composition of the blood itself, and have no reference to the extraneous substances, such as the absorbed materials of the food, which it may contain; neither, indeed, has any complete analysis of these been given.

Comparative analyses of blood in the portal vein and blood in the hepatic veins have also been frequently made, with the view of determining the changes which this fluid undergoes in its transit through the liver. Great diversity, however, is observable in the analyses of these two kinds of blood by different chemists. Part of this diversity is no doubt attributable to the fact pointed out by Bernard, that

unless the portal vein is tied before the liver is removed from the body, hepatic venous blood is very liable to regurgitate into the portal vein, and thus vitiate the result of the analysis. Guarding against this source of error, recent observers seemed to have determined that hepatic venous blood contains less water, albumen, and salts, than the blood of the portal vein; but that it yields a much larger amount of extractive matter, in which, according to Bernard and others, is one constant element, namely, grape-sugar, which is found, whether saccharine or farinaceous matter have been present in the food or not.

Besides the rather wide difference between the composition of the blood of these veins and of others, it must not be forgotten that in its passage through every organ and tissue of the body, the blood's composition must be varying constantly, as each part takes from it or adds to it such matter as it, roughly speaking, wishes either to have or to throw away. Thus the blood of the renal vein has been proved by experiment to contain less water than does the blood of the artery, and doubtless its salts are diminished also. The blood in the renal vein is said, moreover, by Bernard and Brown-Séquard not to coagulate.

This then is an example of the change produced in the blood by its passage through a special excretory organ. But all parts of the body, bones, muscles, nerves, etc., must act on the blood as it passes through them, and leave in it some mark of their action, too slight though it may be, at any given moment, for analysis by means now at our disposal.

On the Gases contained in the Blood.

The gases contained in the blood are carbonic acid, oxygen, and nitrogen, 100 volumes of blood containing from 40 to 50 volumes of these gases collectively.

Arterial blood contains relatively more oxygen and less carbonic acid than venous. But the absolute quantity of carbonic acid is in both kinds of blood greater than that of

the oxygen. The proportion of nitrogen is in both very small.

It is most probable that the carbonic acid of the blood is partly in a state of simple solution, and partly in a state of weak chemical combination. That portion of the carbonic acid which is chemically combined, is contained partly in a bicarbonate of soda, and partly is united with phosphate of the same base. The oxygen is combined chemically with the hæmoglobin of the red corpuscles (pp. 75 and 85).

That the oxygen is absorbed chiefly by the red corpuscles is proved by the fact that while blood is capable of absorbing oxygen in considerable quantity, the serum alone has little or no more power of absorbing this gas than pure water.

Development of the Blood.

In the development of the blood little more can be traced than the processes by which the corpuscles are formed.

The first formed blood-cells of the human embryo differ much in their general characters from those which belong to the latter periods of intra-uterine, and to all periods of extra-uterine life. Their manner of origin differs also, and it will be well perhaps to consider this first.

In the process of development of the embryo, the plan, so to speak, of the heart and chief blood-vessels is first laid out in cells. Thus the heart is at first but a solid mass of cells, resembling those which constitute all other parts of the embryo; and continuous with this are tracts of similar cells—the rudiments of the chief blood-vessels.

The formation of the first blood corpuscles is very simple. While the outermost of the embryonic cells, of which the rudimentary heart and its attendant vessels are composed, gradually develop into the muscular and other tissues which form the walls of the heart and blood-vessels, the inner cells simply separate from each other, and form

blood-cells; some fluid plasma being at the same time secreted. Thus, by the same process, blood is formed, and the originally solid heart and blood-vessels are hollowed out.

The blood-cells produced in this way, are from about $\frac{1}{2500}$ to $\frac{1}{1500}$ of an inch in diameter, mostly spherical, pellucid, and colourless, with granular contents, and a well-marked nucleus. Gradually, they acquire a red colour, at the same time that the nucleus becomes more defined, and the granular matters clears away. Mr. Paget describes them as, at this period, circular, thickly disc-shaped, full-coloured, and, on an average, about $\frac{1}{2500}$ of an inch in diameter; their nuclei, which are about $\frac{1}{5000}$ of an inch in diameter, are central, circular, very little prominent on the surfaces of the cell, and apparently slightly granular or tuberculated.

Before the occurrence, however, of this change—from the colourless to the coloured state—in many instances, probably, during it, and in many afterwards, a process of multiplication takes place by division of the nucleus and subsequently of the cell, into two, and much more rarely,

Fig. 30.*

three or four new cells, which gradually acquire the characters of the original cell from which they sprang. Fig. 30 (B, C, D, E).

Fig. 30. Development of the first set of blood-corpuscles in the

When, in the progress of embryonic development, the liver begins to be formed, the multiplication of blood-cells in the whole mass of blood ceases, according to Kölliker, and new blood-cells are produced by this organ. Like those just described, they are at first colourless and nucleated, but afterwards acquire the ordinary blood-tinge, and resemble very much those of the first set. Like them they may also multiply by division. In whichever way produced, however, whether from the original formative cells of the embryo, or by the liver, these coloured nucleated cells begin very early in fœtal life to be mingled with coloured non-nucleated corpuscles resembling those of the adult, and about the fourth or fifth month of embryonic existence are completely replaced by them.

The manner of origin of these perfect non-nucleated corpuscles must be now considered.

I. *Concerning the Cells from which they arise.*

a. Before Birth.—It is uncertain whether they are derived only from the cells of the lymph, which, at about the period of their appearance, begins to be poured into the blood; or whether they are derived also from the nucleated red cells, which they replace, or also from similar nucleated cells, which Kölliker thinks are produced by the liver during the whole time of fœtal existence.

b. After Birth.—It is generally agreed that after birth the red corpuscles are derived from the smaller of the nucleated lymph or chyle-corpuscles,—*the white corpuscles of the blood.*

II. *Concerning the Manner of their Development.*

There is not perfect agreement among physiologists

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mammalian embryo. A. A dotted, nucleated embryo-cell in process of conversion into a blood-corpuscle: the nucleus provided with a nucleolus. B. A similar cell with a dividing nucleus; at C, the division of the nucleus is complete; at D, the cell also is dividing. E. A blood-corpuscle almost complete, but still containing a few granules. F. Perfect blood-corpuscle.

concerning the process by which lymph-globules or white corpuscles (and in the fœtus, perhaps the red nucleated cells) are transformed into red non-nucleated blood-cells. For while some maintain that the whole cell is changed into a red one by the gradual clearing up of the contents, including the nucleus, it is believed by Mr. Wharton Jones and many others, that only the nucleus becomes the red blood-cell, by escaping from its envelope and acquiring the ordinary blood-tint.

Of these two theories, that which supposes the nucleus of the lymph or chyle globule to be the germ of the future red blood-corpuscle is the theory now generally adopted.

The development of red blood-cells from the corpuscles of the lymph and chyle continues throughout life, and there is no reason for supposing that after birth they have any other origin.

Without doubt, these little bodies have, like all other parts of the organism, a tolerably definite term of existence, and in a like manner die and waste away when the portion of work allotted to them has been performed. Neither the length of their life, however, nor the fashion of their decay, has been yet clearly made out, and we can only surmise that in these things they resemble more or less closely those parts of the body which lie more plainly within our observation.

From what has been said, it will have appeared that when the blood is once formed, its *growth* and *maintenance* are effected by the constant repetition of the development of new portions. In the same proportion that the blood yields its materials for the maintenance and repair of the several solid tissues, and for secretions, so are new materials supplied to it in the lymph and chyle, and by development made like it. The part of the process which relates to the formation of new corpuscles has been described, but it is probably only a small portion of the whole process; for the assimilation of the new materials to the blood must be

perfect, in regard to all those immeasurable minute particulars by which the blood is adapted for the nutrition of every tissue, and the maintenance of every peculiarity of each. How precise the assimilation must be for such an adaptation, may be conceived from some of the cases in which the blood is altered by disease, and by assimilation is maintained in its altered state. For example, by the insertion of vaccine matter, the blood is for a short time manifestly diseased; however minute the portion of virus, it affects and alters, in some way, the whole of the blood. And the alteration thus produced, inconceivably slight as it must be, is long maintained; for even very long after a successful vaccination, a second insertion of the virus may have no effect, the blood being no longer amenable to its influence, because the new blood, formed after the vaccination, is made like the blood as altered by the vaccine virus; in other words, the blood exactly assimilates to its altered self the materials derived from the lymph and chyle. In health we cannot see the precision of the adjustment of the blood to the tissues; but we may imagine it from the small influences by which, as in vaccination, it is disturbed; and we may be sure that the new blood is as perfectly assimilated to the healthy standard as in disease it is assimilated to the most minutely altered standard.*

How far the assimilation of the blood is affected by any formative power which it may possess in common with the solid tissues, we know not. That this possible formative power is, however, if present, greatly ministered to and assisted by the actions of other parts there can be no doubt; as 1*st*, by the digestive and absorbent systems, and probably by the liver, and all of the so-called *vascular* glands; and, 2*ndly*, by the excretory organs, which separate from the blood refuse materials, including in this term not only

* Corresponding facts in relation to the maintenance of the tissues by assimilation will be mentioned in the chapter on NUTRITION.

the waste substance of the tissues, but also such matters as, having been taken with food and drink, may have been absorbed from the digestive canal, and have been subsequently found unfit to remain in the circulating current. And, *3rdly*, the precise constitution of the blood is adjusted by the balance of the nutritive processes for maintaining the several tissues, so that none of the materials appropriate for the maintenance of any part may remain in excess in the blood. Each part, by taking from the blood the materials it requires for its maintenance, is, as has been observed, in the relation of an excretory organ to all the rest; inasmuch as by abstracting the matters proper for its nutrition, it prevents excess of such matters as effectually as if they were separated from the blood and cast out altogether by the excreting organs specially present for such a purpose.

Uses of the Blood.

The *purposes* of the blood, thus developed and maintained, appear, in the perfect state, to be these; *1st*, to be a source whence the various parts of the body may abstract the materials necessary for their nutrition and maintenance; and whence the secreting organs may take the materials for their various secretions; *2nd*, to be a constantly replenished store-house of latent chemical force, which in its expenditure will maintain the heat of the body, or be transformed by the living tissues, and manifested by them in various forms as vital power; *3rd*, to convey oxygen to the several tissues which may need it, either for the discharge of their functions, or for combination with their refuse matter; *4th*, to bring from all parts refuse matters, and convey them to places whence they may be discharged; *5th*, to warm and moisten all parts of the body.

Uses of the various Constituents of the Blood.

Regarding the uses of the various constituents of the

blood it may be said that the matter almost resolves itself into an analysis of the different parts of the body, and of the food and drink which are taken for their nutrition, with a subsequent consideration of how far any given constituent of the blood may be supposed to be on its way to the living tissues, to be incorporated with and nourish them, or, having fulfilled its purpose, to be on its way in a more or less changed condition to the excretory organs to be cast out. It must be remembered, however, that the blood contains also matters which serve by their combustion to produce heat, and, again, others which possibly subserve only a mechanical, although most important, purpose; as for instance the preservation of the due specific gravity of the blood, or some other quality by which it is enabled to maintain its proper relation to the vessels containing it and to the tissues through which it passes. Lastly, among the constituents of the blood, are the gases, oxygen and carbonic acid, and the substances specially adapted to carry them, which can scarcely be said to take part in the nutrition of the body, but are rather the means and evidence of the combustion before referred to, on which, to a great extent, directly or indirectly, all vitality depends.

Albumen.—The albumen, which exists in so large a proportion among the chief constituents of the blood, is without doubt mainly for the nourishment of those textures which contain it or other compounds nearly allied to it. Besides its purpose in nutrition, the albumen of the liquor sanguinis is doubtless of importance also in the maintenance of those essential physical properties of the blood to which reference has been already made.

Fibrin.—It has been mentioned in a previous part of this chapter that the idea of fibrin existing in the blood, as fibrin, is probably founded in error; and that it is formed in the act of coagulation by the union of two substances, which before existed separately (p. 64). In considering, therefore, the functions of fibrin, we may exclude the notion

of its existence, as such, in the blood in a fluid state, and of its use in the nutrition of certain special textures, and look for the explanation of its functions to those circumstances, whether of health or disease, under which it is produced. In hæmorrhage, for example, the formation of fibrin in the clotting of blood, is the means by which, at least for a time, the bleeding is restrained or stopped; and the material which is produced for the permanent healing of the injured part, contains a coagulable material probably identical, or very nearly so, with the fibrin of clotted blood.

Fatty Matters.—The fatty matters of the blood subserve more than one purpose. For while they are the means, at least in part, by which the fat of the body, so widely distributed in the proper adipose and other textures, is replenished, they also, by their union with oxygen, assist in maintaining the temperature of the body. In certain secretions also, notably the milk and bile, fat is an important constituent.

Saline Matter.—The uses of the saline constituents of the blood are, first, to enter into the composition of such textures and secretions as naturally contain them, and, secondly, to assist in preserving the due specific gravity and alkalinity of the blood and, perhaps, also in preventing its decomposition. The phosphate and carbonate of sodium, besides maintaining the alkalinity of the blood, are said especially to preserve the liquidity of its albumen, and to favour its circulation through the capillaries, at the same time that they increase the absorptive power of the serum for gases. But although, from the constant presence of a certain quantity of saline matter in the blood, we may believe that it has these last-mentioned important functions in connection with the blood itself, apart from the nutrition of the body, yet, from the amount which is daily separated by the different excretory organs, and especially by the kidneys, we must also believe that a considerable quantity simply passes through the blood, both from the

food and from the tissues, as a temporary and useless constituent, to be excreted when opportunity offers.

Corpuscles.—The uses of the red corpuscles are probably not yet fully known, but they may be inferred, at least in part, from the composition and properties of their contents. The affinity of hæmoglobin for oxygen has been already mentioned; and the main function of the red corpuscles seems to be the absorption of oxygen in the lungs by means of this constituent, and its conveyance to all parts of the body, especially to those tissues, the nervous and muscular, the discharge of whose functions depends in so great a degree upon a rapid and full supply of this element. The readiness with which hæmoglobin absorbs oxygen, and delivers it up again to a reducing agent, so well shown by the experiments of Prof. Stokes, admirably adapts it for this purpose. How far the red corpuscles are concerned in the nutrition of the tissues is quite unknown.

The relation of the white to the red corpuscles of the blood has been already considered (p. 92); of the functions of the former, other than are concerned in this relationship, nothing is positively known. Recent observations of the migration of the white corpuscles from the interior of the blood-vessels into the surrounding tissues (see Section, On the Circulation in the Capillaries) have, however, opened out a large field for investigation of their probable functions in connection with the nutrition of the textures, in which, even in health, they appear to wander.

CHAPTER VI

CIRCULATION OF THE BLOOD.

The body is divided into two chief cavities—the *chest* or *thorax* and *abdomen*, by a curved muscular partition, called the *diaphragm* (fig. 31). The chest is almost entirely filled by the lungs and heart; the latter being fitted in, so to speak, between the two lungs, nearer the front than the back of the chest, and partly overlapped by them (fig. 31). Each of these organs is contained in a distinct bag, called respectively the right and left pleura and the pericardium, the latter being fibrous in the main, but lined on the inner aspect by a smooth shining epithelial covering, on which can glide, with but little friction, the equally smooth surface of the heart enveloped by it. In fig. 31 the containing bags of pleura and pericardium are supposed to have been removed. Entering the chest from above is a large and long air-tube, called the trachea, which divides into two branches, one for each lung, and through which air passes and repasses in respiration. Springing from the upper part or base of the heart may be seen the large vessels, arteries, and veins, which convey blood either to or from this organ.

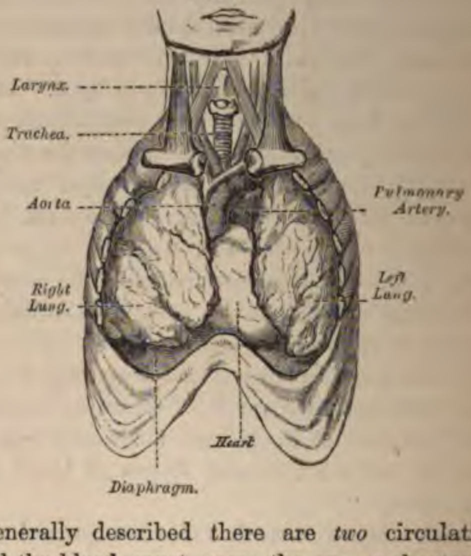
In the living body the heart and lungs are in constant rhythmic movement, the result of which is an unceasing stream of air through the trachea alternately into and out of the lungs, and an unceasing stream of blood into and out of the heart.

It is with this last event that we are concerned especially in this chapter,—with the means, that is to say, by which the blood which at one moment is forced out of the heart, is in a few moments more returned to it, again to depart, and again pass through the body in course of what is

technically called the *circulation*. The purposes for which this unceasing current is maintained, are indicated in the uses of the blood enumerated in the preceding chapter.

The blood is conveyed away from the heart by the *arteries*, and returned to it by the *veins*; the arteries and veins being continuous with each other, at one end by means of the heart, and at the other by a fine network of vessels called the *capillaries*. The blood, therefore, in its passage from the heart passes first into the arteries, then into the capillaries, and lastly into the veins, by which it is conveyed back again to the heart,—thus completing a revolution, or *circulation*.

Fig. 31.*



As generally described there are *two* circulations by which all the blood must pass; the one, a shorter circuit

* Fig. 31. View of heart and lungs *in situ*. The front portion of the chest-wall, and the outer or *parietal* layers of the pleuræ and pericardium have been removed. The lungs are partly collapsed.

from the heart to the lungs and back again; the other and larger circuit, from the heart to all parts of the body and back again; but more strictly speaking, there is only *one* complete circulation, which may be diagrammatically represented by a double loop, as in the accompanying figure.

Fig. 32.*

On reference to this figure and noticing the direction of the arrows which represent the course of the stream of blood, it will be observed that while there is a smaller and a larger circle both of which pass through the heart, yet that these are not distinct, one from the other, but are formed really by one continuous stream, the whole of which must, at one part of its course, pass through the lungs. Subordinate to the two principal circulations, the *pulmonary* and *systemic* as they are named, it will be noticed also in the same figure, that there is another, by which a portion of the stream of blood having been diverted once into the capillaries of the intestinal canal, and some other organs, and gathered up again into a single stream, is a second time divided in its passage through the liver,

* *Fig. 32. Diagram of* the circulation.

before it finally reaches the heart and completes a revolution. This subordinate stream through the liver is called the *portal* circulation.

The principal force provided for constantly moving the blood through this course is that of the muscular substance of the heart; other assistant forces are (2) those of the elastic walls of the arteries, (3) the pressure of the muscles among which some of the veins run, (4) the movements of the walls of the chest in respiration, and probably, to some extent, (5), the interchange of relations between the blood and the tissues which ensues in the capillary system during the nutritive processes. The right direction of the blood's course is determined and maintained by the valves of the heart to be immediately described; which valves open to permit the movement of the blood in the course described, but close when any force tends to move it in the contrary direction.

We shall consider separately each member of the system of organs for the circulation: and first—

The Heart.

The heart is a hollow muscular organ, the interior of which is divided by a partition in such a manner as to form two chief chambers or cavities—right and left. Each of these chambers is again subdivided into an upper and a lower portion called respectively the *auricle* and *ventricle*, which freely communicate one with the other; the aperture of communication, however, being guarded by valvular curtains, so disposed as to allow blood to pass freely from the auricle into the ventricle, but not in the opposite direction. There are thus four cavities altogether in the heart—two auricles and two ventricles; the auricle and ventricle of one side being quite separate from those of the other. The *right* auricle communicates, on the one hand with the veins of the general system, and, on the other, with the right ventricle, while the latter leads directly into the pulmonary artery, the orifice of which is guarded by valves.

The *left* auricle again communicates, on the one hand, with the pulmonary veins, and, on the other, with the left ventricle, while the latter leads directly into the aorta—a large artery which conveys blood to the general system, the orifice of which, like that of the pulmonary artery, is guarded by valves.

The arrangement of the heart's valves is such that the blood can pass only in one definite direction, and this is as follows (fig. 33):—From the right auricle the blood passes into the right ventricle, and thence into the pulmonary artery, by which it is conveyed to the capillaries of the lungs. From the lungs the blood, which is now purified and altered in colour, is gathered by the pulmonary veins and taken to the left auricle. From the left auricle it passes into the left ventricle, and thence into the aorta, by which it is distributed to the capillaries of every portion of the body. The branches of the aorta, from being distributed to the general system, are called *systemic* arteries; and from these the blood passes into the *systemic* capillaries, where it again becomes dark and impure, and thence into the branches of the *systemic* veins, which,

Fig. 33.*

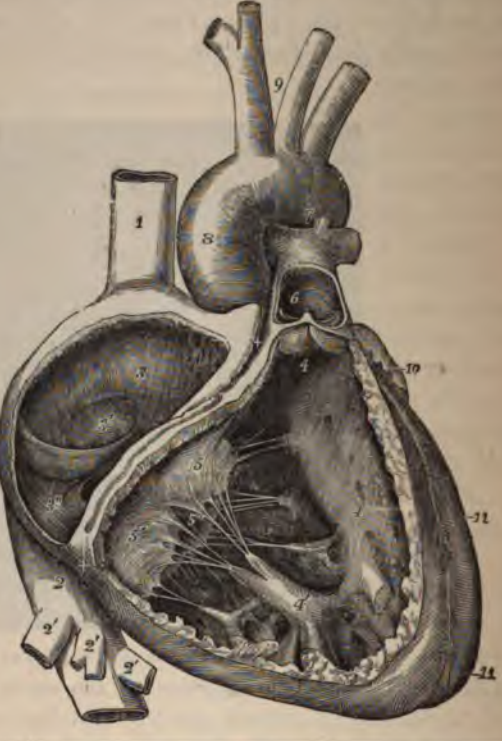
* Fig. 33. Diagram of the circulation through the heart (after Dalton).

forming by their union two large trunks, called the superior and inferior vena cava, discharge their contents into the right auricle, whence we supposed the blood to start (fig. 33).

Structure of the Valves of the Heart.

It will be well now to consider the structure of the

Fig. 34.*



* Fig. 34. The right auricle and ventricle opened, and a part of their right and anterior walls removed, so as to show their interior. ½. —1, superior vena cava; 2, inferior vena cava; 2', hepatic veins cut short; 3, right auricle; 3', placed in the fossa ovalis, below which is the Eustachian valve; 3'', is placed close to the aperture of the coronary

valves of the heart, and the manner in which they perform their function of directing the stream of blood in the course which has been just described. The valve between the right auricle and ventricle is named *tricuspid* (fig. 34), because it presents three principal cusps or pointed portions, and that between the left auricle and ventricle *bicuspid* or *mitral*, because it has two such portions (fig. 35). But in both valves there is between each two principal portions a smaller one; so that more properly, the tricuspid may be described as consisting of six, and the mitral of four, portions. Each portion is of triangular form, its apex and sides lying free in the cavity of the ventricle, and its base, which is continuous with the bases of the neighbouring portions, so as to form an annular membrane around the auriculo-ventricular opening, being fixed to a tendinous ring, which encircles the orifice between the auricle and ventricle, and receives the insertions of the muscular fibres of both. In each principal portion of the valve may be distinguished a middle-piece, extending from its base to its apex, and including about half its width; this piece is thicker, and much tougher and tighter than the border-pieces which are attached loose and flapping at its sides.

While the bases of the several portions of the valves are fixed to the tendinous rings, their ventricular surfaces

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vein; +, +, placed in the auriculo-ventricular groove, where a narrow portion of the adjacent walls of the auricle and ventricle has been preserved; 4, 4, cavity of the right ventricle, the upper figure is immediately below the semilunar valves; 4′, large columna carnea or musculus papillaris; 5, 5′, 5″, tricuspid valve; 6, placed in the interior of the pulmonary artery, a part of the anterior wall of that vessel having been removed, and a narrow portion of it preserved at its commencement where the semilunar valves are attached; 7, concavity of the aortic arch close to the cord of the ductus arteriosus; 8, ascending part or sinus of the arch covered at its commencement by the auricular appendix and pulmonary artery; 9, placed between the innominate and left carotid arteries; 10, appendix of the left auricle; 11, 11, the outside of the left ventricle, the lower figure near the apex. (From Quain's Anatomy.)

and borders are fastened by slender tendinous fibres, the *chordæ tendineæ*, to the walls of the ventricles, the muscular fibres of which project into the ventricular cavity in the

Fig. 35.*

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* Fig. 35. The left auricle and ventricle opened and a part of their anterior and left walls removed so as to show their interior. ½.—The pulmonary artery has been divided at its commencement so as to show the aorta; the opening into the left ventricle has been carried a short distance into the aorta between two of the segments of the semilunar valves; the left part of the auricle with its appendix has been removed.

form of bundles or columns—the *columnæ carneæ.* These columns are not all of them alike, for while some of them are attached along their whole length on one side, and by their extremities, others are attached only by their extremities; and a third set, to which the name *musculi papillares* has been given, are attached to the wall of the ventricle by one extremity only, the other projecting, papilla-like, into the cavity of the ventricle (5, fig. 35), and having attached to it *chordæ tendineæ.* Of the tendinous cords, besides those which pass from the walls of the ventricle and the *musculi papillares*, to the margins of the valves both free and attached, there are some of especial strength, which pass from the same parts to the edges of the middle pieces of the several chief portions of the valve. The ends of these cords are spread out in the substance of the valve, giving its middle piece its peculiar strength and toughness; and from the sides numerous other more slender and branching cords are given off, which are

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The right auricle has been thrown out of view. 1, the two right pulmonary veins cut short; their openings are seen within the auricle; 1′, placed within the cavity of the auricle on the left side of the septum and on the part which forms the remains of the valve of the foramen ovale, of which the crescentic fold is seen towards the left hand of 1′; 2, a narrow portion of the wall of the auricle and ventricle preserved round the auriculo-ventricular orifice; 3, 3′, the cut surface of the walls of the ventricle, seen to become very much thinner towards 3″, at the apex; 4, a small part of the anterior wall of the left ventricle which has been preserved with the principal anterior columna carnea or musculus papillaris attached to it; 5, 5, musculi papillares; 5′, the left side of the septum, between the two ventricles, within the cavity of the left ventricle; 6, 6′, the mitral valve; 7, placed in the interior of the aorta near its commencement and above the three segments of its semilunar valve which are hanging loosely together; 7′, the exterior of the great aortic sinus; 8, the root of the pulmonary artery and its semilunar valves; 8′, the separated portion of the pulmonary artery remaining attached to the aorta by 9, the cord of the ductus arteriosus; 10, the arteries rising from the summit of the aortic arch. (From Quain's Anatomy.)

attached all over the ventricular surface of the adjacent border-pieces of the principal portions of the valves, as well as to those smaller portions which have been mentioned as lying between each two principal ones. Moreover, the *musculi papillares* are so placed that from the summit of each tendinous cords may proceed to the adjacent halves of two of the principal divisions, and to one intermediate or smaller division, of the valve.

It has been already said that while the ventricles communicate, on the one hand, with the auricles, they communicate, on the other, with the large arteries which convey the blood away from the heart; the right ventricle with the pulmonary artery (6, fig. 34), which conveys blood to the lungs, and the left ventricle with the aorta, which distributes it to the general system (7, fig. 35). And as the auriculo-ventricular orifice is guarded by valves, so are also the mouths of the pulmonary artery and aorta (figs. 34, 35).

The valves, three in number, which guard the orifice of each of these two arteries, are called the *semilunar* valves. They are nearly alike on both sides of the heart; but those of the aorta are altogether thicker and more strongly constructed than those of the pulmonary artery. Like the tricuspid and mitral valves, they are formed by a duplicature of the lining membrane of the heart, strengthened by fibrous tissue. Each valve is of semilunar shape, its convex margin being attached to a fibrous ring at the place of junction of the artery to the ventricle, and the concave or nearly straight border being free (fig. 35). In the centre of the free edge of the valve, which contains a fine cord of fibrous tissue, is a small fibrous nodule, the *corpus Arantii*, and from this and from the attached border, fine fibres extend into every part of the mid substance of the valve, except a small lunated space just within the free edge, on each side of the *corpus Arantii*. Here the valve is thinnest, and composed of little more than the endocardium. Thus constructed and attached, the three

semilunar valves are placed side by side around the arterial orifice of each ventricle, so as to form three little pouches, which can be thrown back and flattened by the blood passing out of the ventricle, but which belly out immediately so as to prevent any return (6, fig. 34). This will be again referred to immediately.

The muscular fibres of the heart, unlike those of most involuntary muscles, present a *striated* appearance under the microscope. (See Chapter on Motion.)

THE ACTION OF THE HEART.

The heart's action in propelling the blood consists in the successive alternate contractions and dilatations of the muscular walls of its two auricles and two ventricles. The auricles contract simultaneously; so do the ventricles; their dilatations also are severally simultaneous; and the contractions of the one pair of cavities are synchronous with the dilatations of the other.

The description of the action of the heart may best be commenced at that period in each action which immediately precedes the beat of the heart against the side of the chest, and, by a very small interval more, precedes the pulse at the wrist. For at this time the whole heart is in a passive state, the walls of both auricles and ventricles are relaxed, and their cavities are being dilated. The auricles are gradually filling with blood flowing into them from the veins; and a portion of this blood passes at once through them into the ventricles, the opening between the cavity of each auricle and that of its corresponding ventricle being, during all the pause, free and patent. The auricles, however, receiving more blood than at once passes through them to the ventricles, become, near the end of the pause, fully distended; then, in the end of the pause, they contract and empty their contents into the ventricles. The contraction of the auricles is sudden and very quick; it commences at the entrance of the great veins into them,

and is thence propagated towards the auriculo-ventricular opening; but the last part which contracts is the auricular appendix. The effect of this contraction of the auricles is to propel nearly the whole of their blood into the ventricles. The reflux of blood into the great veins is resisted not only by the mass of blood in the veins and the force with which it streams into the auricles, but also by the simultaneous contraction of the muscular coats with which the large veins are provided for some distance before their entrance into the auricles; a resistance which, however, is not so complete but that a small quantity of blood does regurgitate, *i.e.*, flow backwards into the veins, at each auricular contraction. The effect of this regurgitation from the right auricle is limited by the valves at the junction of the subclavian and internal jugular veins, beyond which the blood cannot move backwards; and the coronary vein, or vein which brings back to the right auricle the blood which has circulated in the substance of the heart, is preserved from it by a valve at its mouth.

The blood which is thus driven, by the contraction of the auricles, into the corresponding ventricles, being added to that which had already flowed into them during the heart's pause, is sufficient to complete the dilatation or diastole of the ventricles. Thus distended, they immediately contract: so immediately, indeed, that their contraction, or systole, looks as if it were continuous with that of the auricles. This has been graphically described by Harvey in the following passage:—"These two motions, one of the ventricles, another of the auricles, take place consecutively, but in such a manner that there is a kind of harmony, or rhythm, present between them, the two concurring in such wise that but one motion is apparent; especially in the warmer blooded animals, in which the movements in question are rapid. Nor is this for any other reason than it is in a piece of machinery, in which, though one wheel gives motion to another, yet all the wheels seem to move simul-

taneously; or in that mechanical contrivance which is adapted to fire-arms, where the trigger being touched, down comes the flint, strikes against the steel, elicits a spark, which, falling among the powder, it is ignited, upon which the flame extends, enters the barrel, causes the explosion, propels the ball, and the mark is attained—all of which incidents by reason of the celerity with which they happen, seem to take place in the twinkling of an eye." The ventricles contract much more slowly than the auricles, and in their contraction, probably always thoroughly empty themselves, differing in this respect from the auricles, in which, even after their complete contraction, a small quantity of blood remains. The form and position of the fleshy columns on the internal walls of the ventricle appear, indeed, especially adapted to produce this obliteration of their cavities during their contraction; and the completeness of the closure may often be observed on making a transverse section of a heart shortly after death, in any case in which the contraction of the *rigor mortis* is very marked. In such a case, only a central fissure may be discernible to the eye in the place of the cavity of each ventricle.

At the same time that the walls of the ventricles contract, the fleshy columns, and especially those of them called the *musculi papillares*, contract also, and assist in bringing the margins of the auriculo-ventricular valves into apposition, so that they close the auriculo-ventricular openings, and prevent the backward passage of the blood into the auricles (p. 113). The whole force of the ventricular contraction is thus directed to the propulsion of the blood through their arterial orifices. During the time which elapses between the end of one contraction of the ventricles, and the commencement of another, the communication between them and the great arteries—the aorta on the left side, the pulmonary artery on the right—is closed by the three semilunar valves situated at the orifice of each vessel. But the force with which the current of

blood is propelled by the contraction of the ventricle separates these valves from contact with each other, and presses them back against the sides of the artery, making a free passage for the stream of blood. Then, as soon as the ventricular contraction ceases, the elastic walls of the distended artery recoil, and by pressing the blood behind the valves, force them down towards the centre of the vessel, and spread them out so as to close the orifice and prevent any of the blood flowing back into the ventricles (p. 118).

As soon as the auricles have completed their contraction they begin again to dilate, and to be refilled with blood, which flows into them in a steady stream through the great venous trunks. They are thus filling during all the time in which the ventricles are contracting; and the contraction of the ventricles being ended, these also again dilate, and receive again the blood that flows into them from the auricles. By the time that the ventricles are thus from one-third to two-thirds full, the auricles are distended; these, then suddenly contracting, fill up the ventricles, as already described.

If we suppose a cardiac revolution, which includes the contraction of the auricles, the contraction of the ventricles, and their repose, to occupy rather more than a second, the following table will represent, in tenths of a second, the time occupied by the various events we have considered.

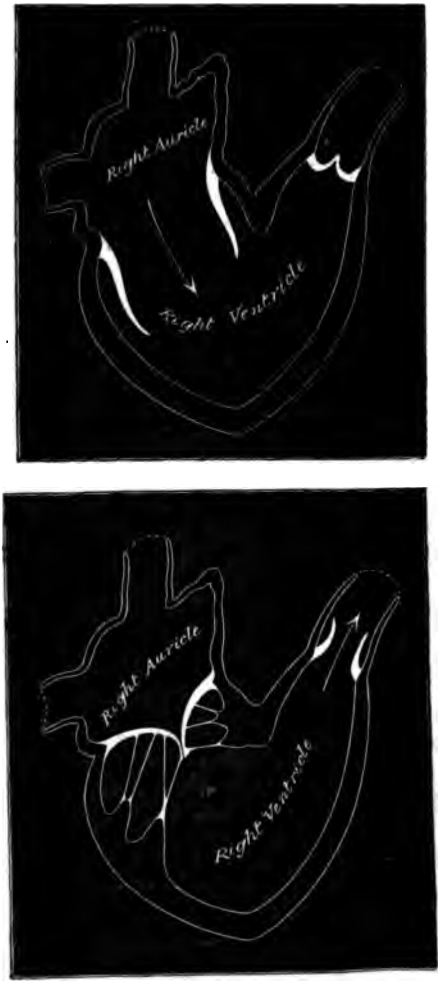
Contraction of Auricles . .	1 +	Repose of Auricles . .	10=11
,, Ventricles .	4 +	,, Ventricles .	7=11
Repose (no contraction of either auricles or ventricles)	6 +	Contraction (of either auricles or ventricles)	5=11
	— 11		

Action of the Valves of the Heart.

The periods in which the several valves of the heart are in action may be connected with the foregoing table; for the auriculo-ventricular valves are closed, and the arterial valves are open during the whole time of the ventricular contraction, while, during the dilatation and distension of

the ventricles the latter valves are shut, the former open. Each half or side of the heart, through the action of its valves, may be compared with a kind of forcing pump, like the common enema-syringe with two valves, of which one admits the fluid on raising the piston, but is closed again when the piston is forced down; while the other opens for the escape of the fluid, but closes when the piston is raised, so as to prevent the regurgitation of the fluid already forced through it. The ventricular dilatation is here represented by the raising-up of the piston; the valve thus admitting fluid represents the auriculo-ventricular valve, which is closed

Fig. 36.*



* Fig. 36. Diagrams of valves of the heart (after Dalton).

again when the piston is forced down, *i.e.*, when the ventricle contracts, and the other, *i.e.*, the arterial, valve opens. The diagrams on the preceding page illustrate this very well.

During auricular contraction, the force of the blood propelled into the ventricle is transmitted in all directions, but being insufficient to raise the semilunar valves, it is expended in distending the ventricle, and in raising and gradually closing the auriculo-ventricular valves, which, when the ventricle is full, form a complete septum between it and the auricle. This elevation of the auriculo-ventricular valves is, no doubt, materially aided by the action of the elastic tissue which Dr. Markham has shown to exist so largely in their structure, especially on the auricular surface. When the ventricle contracts, the edges of the valves are maintained in apposition by the simultaneous contraction of the *musculi papillares*, which are enabled thus to act by the arrangement of their tendinous cords just mentioned. In this position the segments of the valves are held secure, even though the form and size of the orifice and the ventricle may change during the continued contraction; for the border pieces are held by their mutual apposition and the equal pressure of the blood on their ventricular surfaces; and the middle pieces are secure by their great strength, and by the attachment of the tendinous cords along their margins, these cords being always held tight by the contraction of the *musculi papillares.* A peculiar advantage, derived from the projection of these columns into the cavity of the ventricle, seems to be, that they prevent the valve from being converted into the auricle; for, when the ventricle contracts, and the parts of its walls to which, through the medium of the columns, the tendinous cords are affixed, approach the auriculo-ventricular orifices, there would be a tendency to slackness of the cords, and the valves might be everted, if it were not that while the wall of the ventricle is drawn towards the orifice,

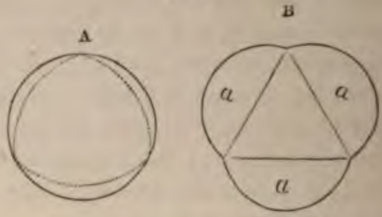
the end of the simultaneously contracting fleshy column is drawn away from it, and the cords are held tight.

What has been said applies equally to the auriculo-ventricular valves on both sides of the heart, and of both alike the closure is generally complete every time the ventricles contract. But in some circumstances, the closure of the tricuspid valve is not complete, and a certain quantity of blood is forced back into the auricle: and, since this may be advantageous, by preventing the over-filling of the vessels of the lungs, it has been called the *safety-valve action* of this valve (Hunter, Wilkinson King). The circumstances in which it usually happens are those in which the vessels of the lung are already full enough when the right ventricle contracts, as *e. g.*, in certain pulmonary diseases, in very active exertion, and in great efforts. In these cases, perhaps, because the right ventricle cannot contract quickly or completely enough, the tricuspid valve does not completely close, and the regurgitation of blood may be indicated by a pulsation in the jugular veins synchronous with that in the carotid arteries.

The *arterial* or *semilunar* valves are, as already said, brought into action by the pressure of the arterial blood forced back towards the ventricles, when the elastic walls of the arteries recoil after being dilated by the blood propelled into them in the previous contraction of the ventricle. The dilatation of the arteries is, in a peculiar manner, adapted to bring the valves into action. The lower borders of the semilunar valves are attached to the inner surface of a tendinous ring, which is, as it were, inlaid, at the orifice of the artery, between the muscular fibres of the ventricle and the elastic fibres of the walls of the artery. The tissue of this ring is tough, does not admit of extension under such pressure as it is commonly exposed to; the valves are equally inextensile, being, as already mentioned, formed of tough, close-textured, fibrous tissue, with strong inter-woven cords, and covered with *endocardium*. Hence, when

the ventricle propels blood through the orifice and into the canal of the artery, the lateral pressure which it exercises is sufficient to dilate the walls of the artery, but not enough to stretch in an equal degree, if at all, the unyielding valves and the ring to which their lower borders are attached. The effect, therefore, of each such propulsion of blood from the ventricle is, that the wall of the first portion of the artery is dilated into three pouches behind the valves, while the free margins of the valves, which had previously lain in contact with the inner surface of the artery (as at A, fig. 37), are drawn inward towards its

Fig. 37.*



centre (fig. 37, B). Their positions may be explained by the foregoing diagrams, in which the continuous lines represent a transverse section of the arterial walls, the dotted ones the edges of the valves, firstly, when the valves are in contact with the walls (A), and, secondly, when the walls being dilated, the valves are drawn away from them (B).

This position of the valves and arterial walls is retained so long as the ventricle continues in contraction: but, so

* Fig. 37. Sections of aorta, to show the action of the semilunar valves. A is intended to show the valves, represented by the dotted lines, in contact with the arterial walls, represented by the continuous outer line. B (after Hunter) shows the arterial wall distended into three pouches (*a*), and drawn away from the valves which are straightened into the form of equilateral triangle, as represented by the dotted lines.

soon as it relaxes, and the dilated arterial walls can recoil by their elasticity, they press the blood as well towards the ventricles as onwards in the course of the circulation. Part of the blood thus pressed back lies in the pouches (*a*, fig. 37, B) between the valves and the arterial walls; and the valves are by it pressed together till their thin lunated margins meet in three lines radiating from the centre to the circumference of the artery (7 and 8, fig. 38).

*Fig. 38.**

* Fig. 38. View of the base of the ventricular part of the heart, showing the relative position of the arterial and auriculo-ventricular orifices.—⅔. The muscular fibres of the ventricles are exposed by the removal of the pericardium, fat, blood-vessels, etc.; the pulmonary artery and aorta have been removed by a section made immediately beyond the attachment of the semilunar valves, and the auricles have been removed immediately above the auriculo-ventricular orifices. The semilunar and auriculo-ventricular valves are in the nearly closed condition. 1, 1, the base of the right ventricle; 1', the conus arteriosus; 2, 2, the base of the left ventricle; 3, 3, the divided wall of the right auricle; 4, that of the left; 5, 5', 5'', the tricuspid valve; 6, 6', the mitral valve. In the angles beween these segments are seen the smaller fringes frequently observed; 7, the anterior part of the pulmonary artery; 8, placed upon the posterior part of the root of the aorta; 9, the right, 9', the left coronary artery. (From Quain's Anatomy.)

Mr. Savory has clearly shown that this pressure of the blood is not entirely sustained by the valves alone, but in part by the muscular substance of the ventricle. Availing himself of a method of dissection hitherto apparently overlooked, namely, that of making vertical sections (fig. 39) through various parts of the tendinous rings, he has been enabled to show clearly that the aorta and pulmonary artery, expanding towards their termination, are situated upon the *outer* edge of the thick upper border of the ventricles, and that consequently the portion of each semilunar valve adjacent to the vessel passes over and rests upon the muscular substance—being thus supported, as it were, on a kind of muscular floor formed by the free border of the ventricle. The result of this arrangement will be that the reflux of the blood will be most efficiently sustained by the ventricular wall.†

Fig. 39*.

The effect of the blood's pressure on the valves is, as said, to cause their margins to meet in three lines radiating from the centre to the circumference (7 and 8, fig. 38). The contact of the valves in this position, and the complete closure of the arterial orifice, are secured by the peculiar construction of their borders before mentioned. Among the cords which are interwoven in the substance of the valves, are two of greater strength and prominence than the rest; of which one extends along the free border of each valve, and

* Fig. 39. Vertical section through the aorta at its junction with the left ventricle. 1. Section of arterial coat. 2. Section of valve. 3. Section of ventricle.

† Mr. Savory's preparations, illustrating this and other points in relation to the structure and functions of the valves of the heart, are in the museum of St. Bartholomew's Hospital.

the other forms a double curve or festoon just below the free border. Each of these cords is attached by its outer extremities to the outer end of the free margin of its valve, and in the middle to the corpus Arantii; they thus enclose a lunated space from a line to a line and a half in width, in which space the substance of the valve is much thinner and more pliant than elsewhere. When the valves are pressed down, all these parts or spaces of their surfaces come into contact, and the closure of the arterial orifice is thus secured by the apposition not of the mere edges of the valves, but of all those thin lunated parts of each, which lie between the free edges and the cords next below them. These parts are firmly pressed together, and the greater the pressure that falls on them, the closer and more secure is their apposition. The corpora Arantii meet at the centre of the arterial orifice when the valves are down, and they probably assist in the closure; but they are not essential to it, for, not unfrequently, they are wanting in the valves of the pulmonary artery, which are then extended in larger, thin, flapping margins. In valves of this form, also, the inlaid cords are less distinct than in those with corpora Arantii; yet the closure by contact of their surfaces is not less secure.

Sounds of the Heart.

When the ear is placed over the region of the heart, two sounds may be heard at every beat of the heart, which follow in quick succession, and are succeeded by a pause or period of silence. The first sound is dull and prolonged; its commencement coincides with the impulse of the heart, and just precedes the pulse at the wrist. The second is a shorter and sharper sound, with a somewhat flapping character, and follows close after the arterial pulse. The period of time occupied respectively by the two sounds taken together, and by the pause, are almost exactly equal.

The relative length of time occupied by each sound, as compared with the other, is a little uncertain. The difference may be best appreciated by considering the different forces concerned in the production of the two sounds. In one case there is a strong, comparatively slow, contraction of a large mass of muscular fibres, urging forward a certain quantity of fluid against considerable resistance; while in the other it is a strong but shorter and sharper recoil of the elastic coat of the large arteries,—shorter because there is no resistance to the flapping back of the semilunar valves, as there was to their opening. The difference may be also expressed, as Dr. C. J. B. Williams has remarked, by saying the words *lubb—dup.*

The events which correspond, in point of time, with the first sound, are the contraction of the ventricles, the first part of the dilatation of the auricles, the closure of the auriculo-ventricular valves, the opening of the semilunar valves, and the propulsion of blood into the arteries. The sound is succeeded, in about one-thirtieth of a second, by the pulsation of the facial artery, and in about one-sixth of a second, by the pulsation of the arteries at the wrist. The second sound, in point of time, immediately follows the cessation of the ventricular contraction, and corresponds with the closure of the semilunar valves, the continued dilatation of the auricles, the commencing dilatation of the ventricles, and the opening of the auriculo-ventricular valves. The pause immediately follows the second sound, and corresponds in its first part with the completed distension of the auricles, and in its second with their contraction, and the distension of the ventricles, the auriculo-ventricular valves being all the time open, and the arterial valves closed.

The chief cause of the first sound of the heart appears to be the vibration of the auriculo-ventricular valves, and also, but to a less extent, of the ventricular walls, and coats of the aorta and pulmonary artery, all of which parts

are suddenly put into a state of tension at the moment of ventricular contraction.

This view, long ago advanced by Dr. Billing, is supported by the fact observed by Valentin, that if a portion of a horse's intestine, tied at one end, be moderately filled with water, without any admixture of air, and have a syringe containing water fitted to the other end, the first sound of the heart is exactly imitated by forcing in more water, and thus suddenly rendering the walls of the intestine more tense.

The cause of the *second* sound is more simple than that of the first. It is probably due entirely to the sudden closure and consequent vibration of the semilunar valves when they are pressed down across the orifices of the aorta and pulmonary artery; for, of the other events which take place during the second sound, none is calculated to produce sound. The influence of the valves in producing the sound, is illustrated by the experiment already quoted from Valentin, and from others performed on large animals, such as calves, in which the results could be fully appreciated. In these experiments two delicate curved needles were inserted, one into the aorta, and another into the pulmonary artery, below the line of attachment of the semilunar valves, and, after being carried upwards about half an inch, were brought out again through the coats of the respective vessels, so that in each vessel one valve was included between the arterial walls and the wire. Upon applying the stethoscope to the vessels, after such an operation, the second sound had ceased to be audible. Disease of these valves, when so extensive as to interfere with their efficient action, also often demonstrates the same fact by modifying or destroying the distinctness of the second sound.

One reason for the second sound being a clearer and sharper one than the first may be, that the semilunar valves are not covered in by the thick layer of fibres

composing the walls of the heart to such an extent as are the *auriculo-ventricular*. It might be expected therefore that their vibration would be more easily heard through a stethoscope applied to the walls of the chest.

The contraction of the auricles which takes place in the end of the pause is inaudible outside the chest, but may be heard, when the heart is exposed and the stethoscope placed on it, as a slight sound preceding and continued into the louder sound of the ventricular contraction.

The Impulse of the Heart.—At the commencement of each ventricular contraction, the heart may be felt to beat with a slight shock or *impulse* against the walls of the chest. This impulse is most evident in the space between the fifth and sixth ribs, between one and two inches to the left of the sternum. The force of the impulse, and the extent to which it may be perceived beyond this point, vary considerably in different individuals, and in the same individuals under different circumstances. It is felt more distinctly, and over a larger extent of surface, in emaciated than in fat and robust persons, and more during a forced expiration than in a deep inspiration; for, in the one case, the intervention of a thick layer of fat or muscle between the heart and the surface of the chest, and in the other the inflation of the portion of lung which overlaps the heart, prevents the impulse from being fully transmitted to the surface. An excited action of the heart, and especially a hypertrophied condition of the ventricles, will increase the impulse, while a depressed condition, or an atrophied state of the ventricular walls, will diminish it.

The impulse of the heart is probably the result, in part, of a tilting forwards of the apex, so that it is made to strike against the walls of the chest. This tilting movement is thought to be effected by the contraction of the spiral muscular fibres of the ventricles, and especially of certain of these fibres which, according to Dr. Reid, arise from the base of the ventricular septum, pass downwards

and forwards, forming part of the septum, then emerge and curve spirally around the apex and adjacent portion of the heart. The whole extent of the movement thus produced is, however, but slight. The condition, which, no doubt, contributes most to the occurrence and character of the impulse of the heart, is its change of shape; for, during the contraction of the ventricles, and the consequent approximation of the base towards the apex, the heart becomes more globular, and bulges so much, that a distinct impulse is felt when the finger is placed over the bulging portion, either at the front of the chest, or under the diaphragm. The production of the impulse is, perhaps, further assisted by the tendency of the aorta to straighten itself and diminish its curvature when distended with the blood impelled by the ventricle; and by the elastic recoil of all the parts about the base of the heart, which, according to the experiments of Kurschner, are stretched downward and backward by the blood flowing into the auricles and ventricles during the dilatation of the latter, but recover themselves when, at the beginning of the contraction of the ventricles, the flow through the auriculo-ventricular orifices is stopped. But these last-mentioned conditions can only be accessory in the perfect state of things; for the same tilting movement of the heart ensues when its apex is cut off, and when, therefore, no tension or change of form can be produced by the blood.

Although what we generally recognise as the impulse of the heart is produced in the way just mentioned, the beat is not so simple a shock as it may seem when only felt by the finger. By means of an instrument called a *cardiograph*, it may be shown to be compounded of three or four shocks, of which the finger can only feel the greatest.

The cardiograph is a tube, dilated at one end into a cup or funnel, either open-mouthed or closed by an elastic membrane, while at the other it communicates with the interior of a small metal drum, one side of which is

formed by an elastic membrane, on which rests a finely-balanced lever, like that of the sphygmograph (fig. 42.)

When used, the cup at one end of the tube is placed immediately over the part of the chest-wall at which the apex of the heart beats; while the lever on the drum is placed in contact with a registering apparatus. (See description of sphygmograph, p. 147.) When the heart beats, the shock communicates a series of impulses to the column of air in the now closed tube, with the effect of raising the elastic wall of the drum, and of course the lever which is attached to it. A *tracing* of the heart's impulse is thus obtained in the same way as that of the pulse, in the arteries (figs. 44 and 45).

The tracing shows that besides the strong beat which alone the finger recognises as the impulse of the heart, and which is caused by the contraction of the ventricles, there are other minor shocks which are imperceptible to the touch. The latter, M. Marey, by experiments on the lower animals, has proved to be the results, respectively, of the contraction of the auricles, and of the closure of the auriculo-ventricular and semilunar valves.

Frequency and Force of the Heart's Action.

The frequency with which the heart performs the actions we have described, may be counted by the pulses at the wrist, or in any other artery; for these correspond with the contractions of the ventricles.

The heart of a healthy adult man in the middle period of life, acts from seventy to seventy-five times in a minute. The frequency of the heart's action gradually diminishes from the commencement to near the end of life, but is said to rise again somewhat in extreme old age, thus:—

In the embryo the average number of pulses in a minute is	150
Just after birth . . . . . . from	140 to 130
During the first year	130 to 115
During the second year	115 to 100
During the third year	100 to 90
About the seventh year	90 to 85
About the fourteenth year, the average number of pulses in a minute is from . . .	85 to 80
In adult age	80 to 70
In old age	70 to 60
In decrepitude	75 to 65

In persons of sanguine temperament, the heart acts somewhat more frequently than in those of the phlegmatic; and in the female sex more frequently than in the male.

After a meal its action is accelerated, and still more so during bodily exertion or mental excitement; it is slower during sleep. The effect of disease in producing temporary increase or diminution of the heart's action is well known. From the observation of several experimenters, it appears that, in the state of health, the pulse is most frequent in the morning, and becomes gradually slower as the day advances: and that this diminution of frequency is both more regular and more rapid in the evening than in the morning. It is found, also, that as a general rule, the pulse, especially in the adult male, is more frequent in the standing than in the sitting posture, and in the latter than in the recumbent position; the difference being greatest between the standing and the sitting posture. The effect of change of posture is greater as the frequency of the pulse is greater, and, accordingly, is more marked in the morning than in the evening. Dr. Guy, by supporting the body in different postures, without the aid of muscular effort of the individual, has proved that the increased frequency of the pulse in the sitting and standing positions is dependent upon the muscular exertion engaged in maintaining them; the usual effect of these postures on the

pulse being almost entirely prevented when the usually attendant muscular exertion was rendered unnecessary. The effect of food, like that of change of posture, is greater in the morning than in the evening. According to Parrot, the frequency of the pulse increases in a corresponding ratio with the elevation above the sea; and Dr. Frankland informed the author, that at the summit of Mont Blanc his pulse was about double the ordinary standard all the time he was there. After six hours' perfect rest and sleep at the top, it was 120, on descending to the corridor it fell to 108, at the Grands Mulets it was 88, at Chamounix 56; normally, his pulse is 60.

In health there is observed a nearly uniform relation between the frequency of the pulse and of the respirations; the proportion being, on an average, one of the latter to three or four of the former. The same relation is generally maintained in the cases in which the pulse is naturally accelerated, as after food or exercise; but in disease this relation usually ceases to exist. In many affections accompanied with increased frequency of the pulse, the respiration, is, indeed, also accelerated, yet the degree of its acceleration bears no definite proportion to the increased number of the heart's actions: and in many other cases, the pulse becomes more frequent without any accompanying increase in the number of respirations; or, the respiration alone may be accelerated, the number of pulsations remaining stationary, or even falling below the ordinary standard. (On the whole of this subject the article *Pulse*, by Dr. Guy, in the Cyclopædia of Anatomy and Physiology, may be advantageously consulted.)

The *force* with which the left ventricle of the heart contracts is about double that exerted by the contraction of the right: being equal (according to Valentin) to about $\frac{1}{50}$th of the weight of the whole body, that of the right being equal only to $\frac{1}{100}$th of the same. This difference in the amount of force exerted by the contraction of the two

ventricles, results from the walls of the left ventricle being about twice as thick as those of the right. And the difference is adapted to the greater degree of resistance which the left ventricle has to overcome, compared with that to be overcome by the right: the former having to propel blood through every part of the body, the latter only through the lungs.

The force exercised by the auricles in their contraction has not been determined. Neither is it known with what amount of force either the auricles or the ventricles dilate; but there is no evidence for the opinion, that in their dilatation they can materially assist the circulation by any such action as that of a sucking-pump, or a caoutchouc bag, in drawing blood into their cavities. That the force which the ventricles exercise in dilatation is very slight, has been proved by Oesterreicher. He removed the heart of a frog from the body, and laid upon it a substance sufficiently heavy to press it flat, and yet so small as not to conceal the heart from view; he then observed that during the contraction of the heart, the weight was raised; but that during its dilatation, the heart remained flat. And the same was shown by Dr. Clendinning, who, applying the points of a pair of spring callipers to the heart of a live ass, found that their points were separated as often as the heart swelled up in the contraction of the ventricles, but approached each other by the force of the spring when the ventricles dilated. Seeing how slight the force exerted in the dilatation of the ventricles is, it has been supposed that they are only dilated by the pressure of the blood impelled from the auricles; but that both ventricles and auricles dilate spontaneously is proved by their continuing their successive contractions and dilatations when the heart is removed, or even when they are separated from one another, and when therefore no such force as the pressure of blood can be exercised to dilate them. By such spontaneous dilatation they at least offer no resistance to the

influx of blood, and save the force which would otherwise be required to dilate them.

The *capacity* of the two ventricles is probably exactly the same. It is difficult to determine with certainty how much this may be; but, taking the mean of various estimates, it may be inferred that each ventricle is able to contain on an average, about three ounces of blood, the whole of which is impelled into their respective arteries at each contraction. The capacity of the auricles is rather less than that of the ventricles: the thickness of their walls is considerably less. The latter condition is adapted to the small amount of force which the auricles require in order to empty themselves into their adjoining ventricles; the former to the circumstance of the ventricles being partly filled with blood before the auricles contract.

Cause of the Rhythmic Action of the Heart.

It has been attempted in various ways to account for the existence and continuance of the rhythmic movements of the heart. By some it has been supposed that the contact of blood with the lining membrane of the cavities of the heart, furnishes a stimulus, in answer to which the walls of these cavities contract. But the fact that the heart, especially in Amphibia and fishes, will continue to contract and dilate regularly and in rhythmic order after it is removed from the body, completely emptied of blood, and even placed in a vacuum where it cannot receive the stimulus of the atmospheric air, is a proof that even if the contact of blood be the ordinary stimulus to the heart's contraction, it cannot alone be an explanation of its rhythmic motion.

The influence of the mind, and of some affections of the brain and spinal cord upon the action of the heart, proves that it is not altogether, or at all times, independent of the cerebro-spinal nervous system. Yet the numerous experiments instituted for the purpose of determining the

exact relation in which the heart stands towards this system, have failed to prove that the action is directly governed under ordinary circumstances by the power of any portion of the brain or spinal cord. Sudden destruction of either the brain or spinal cord alone, or of both together, produces, immediately, a temporary interruption or cessation of the heart's action: but this appears to be only an effect of the *shock* of so severe an injury; for, in some such cases, the movements of the heart are subsequently resumed, and if artificial respiration be kept up, may continue for a considerable time; and may then again be arrested by a violent shock applied through an injury of the stomach. While, therefore, we must admit an indirect or occasional influence exercised by, or through, the brain and spinal cord upon the movements of the heart, and may believe this influence to be the greater the more highly the several organs are developed, yet it is clear that we cannot ascribe the regular determination and direction of the movements to these nervous centres.

The persistence of the movements of the heart in their regular rhythmic order, after its removal from the body, and their capability of being then re-excited by an ordinary stimulus after they have ceased, prove that the cause of these movements must be resident within the heart itself. And it seems probable, from the experiments and observations of various observers, that it is connected with the existence of numerous minute ganglia of the sympathetic nervous system, which, with connecting nerve-fibres, are distributed through the substance of the heart. These ganglia appear to act as so many centres or organs for the production of motor impulses; while the connecting nerve-fibres unite them into one system, and enable them to act in concert and direct their impulses so as to excite in regular series the successive contractions of the several muscles of the heart. The mode in which ganglia thus act as centres and co-ordinators of nervous power will be

described in the chapter on the NERVOUS SYSTEM; and it will appear probable that the chief peculiarity of the heart, in this respect, is due to the number of its ganglia, and the apparently equal power which they all exercise; so that there is no one part of the heart whose action, more than another's, determines the actions of the rest. Thus, if the heart of a reptile be bisected, the rhythmic, successive actions of auricle and ventricle will go on in both halves: we therefore cannot say that the action of the right side determines or regulates that of the left, or *vice versâ;* and we must suppose that when they act together in the perfect heart, it is because they are both, as it were, set to the same time. Neither can we say that the auricles determine the action of the ventricles; for, if they are separated, they will both contract and dilate in regular, though not necessarily similar, succession. A fact pointed out by Mr. Malden shows how the several portions of each cavity are similarly adjusted to act alike, yet independently of each other. If a point of the surface of the ventricle of a turtle's or frog's heart be irritated, it will immediately contract, and very quickly afterwards all the rest of the ventricle will contract; but, at the close of this general contraction, the part that was irritated and contracted first, is slightly distended or pouched out, showing that it was adjusted to contract in, and for only, a certain time, and that therefore as it began to contract first, so it began to dilate first.

The best interpretation, perhaps, yet given of it, and of rhythmic processes in general, is that by Mr. Paget, who regards them as dependent on rhythmic nutrition, *i.e.*, on a method of nutrition in which the acting parts are gradually raised, with time-regulated progress, to a certain state of instability of composition, which then issues in the discharge of their functions, *e.g.*, of nerve-force in the case of the cardiac ganglia, by which force the muscular walls are excited to contraction. According to this view, there is

in the nervous ganglia of the heart, and in all parts originating rhythmic processes, the same alternation of periods of action with periods of repose, during which the waste in the structure is repaired, as is observed in most of, if not all, the organic phenomena of life. All organic processes seem to be regulated with exact observance of time; and rhythmic nutrition and action, as exhibited in the action of the heart, are but well-marked examples of such chronometric arrangement.

We may conclude, then, that the nervous ganglia in the heart's substance are the immediate regulators of the heart's action, but that they are themselves liable to influences conveyed from without, through branches of the pneumogastric and sympathetic nerves.

The pneumogastric nerves are the media of an *inhibitory* or restraining influence over the action of the heart; for when by section their influence is withdrawn, the pulsations of the organ are increased in frequency and strength; while an opposite effect is produced by stimulating them, —the transmission of an electric current of even moderate strength diminishing the pulsations, or stopping them altogether. Stimulation of the sympathetic nerves, on the other hand, accelerates and strengthens the heart's action.

Various theories have been proposed to account for these peculiar results, but none of them are very satisfactory, and it is probable that many more facts must be discovered before any theory on the subject can be permanently maintained.

The connection of the action of the heart with the other organs, and the influences to which it is subject through them, are explicable from the connection of its nervous system with the other ganglia of the sympathetic, and with the brain and spinal cord through, chiefly, the pneumogastric nerves. But this influence is proved in a much more striking manner by the phenomena of disease than by any experimental or other physiological observations.

The influence of a shock in arresting or modifying the action of the heart,—its very slow action after compression of the brain, or injury to the cervical portion of the spinal cord, — its irregularities and palpitations in dyspepsia and hysteria,—are better evidence for the connection of the heart with the other organs through the nervous system, than are any results obtained by experiments.

Effects of the Heart's Action.

That the contractions of the heart supply alone a sufficient force for the circulation of the blood, appears to be established by the results of several experiments, of which the following is one of the most conclusive:—Dr. Sharpey injected bullock's blood into the thoracic aorta of a dog recently killed, after tying the abdominal aorta above the renal arteries, and found that, with a force just equal to that by which the ventricle commonly impels the blood in the dog, the blood which he injected into the aorta passed in a free stream out of the trunk of the vena cava inferior. It thus traversed both the systemic and hepathic capillaries; and when the aorta was not tied above the renals, blood injected under the same pressure flowed freely through the vessels of the lower extremities. A pressure equal to that of one and a half or two inches of mercury was, in the same way, found sufficient to propel blood through the vessels of the lungs.

But although it is probably true that the heart's action alone is sufficient to ensure the circulation, yet there exist several other forces which are, as it were, supplementary to the action of the heart, and assist it in maintaining the circulation. The principal of these supplemental forces have been already alluded to, and will now be more fully pointed out.

THE ARTERIES.

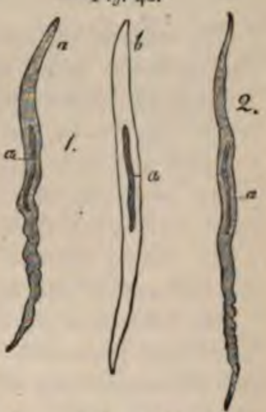
The walls of the arteries are composed of three principal coats, termed the *external* or *tunica adventitia*, the *middle*, and the *internal*, while the latter is lined within by a single layer of tesselated epithelium.

The external coat or tunica adventitia, the strongest and toughest part of the wall of the artery, is formed of areolar tissue, with which is mingled throughout a network of elastic fibres. At the inner part of this outer coat the elastic network forms in most arteries so distinct a layer as to be sometimes called the *external elastic coat.*

The *middle coat* is composed of both muscular and elastic fibres.

The former, which are of the pale or unstriped variety (see Chapter on Motion), are arranged for the most part transversely to the long axis of the artery; while the elastic element, taking also a transverse direction, is disposed in the form of closely interwoven and branching fibres, which intersect in all parts the layers of muscular fibre. In arteries of various size there is a difference in the proportion of the muscular and elastic element, elastic tissue preponderating in the largest arteries, while this condition is reversed in those of medium and small size.

Fig. 40.*



The *internal* arterial coat is formed by layers of elastic tissue, consisting in part of coarse longitudinal branching fibres, and in part of a very thin and brittle membrane which possesses little elasticity, and is thrown into folds

* Fig. 40. Muscular fibre-cells from human arteries, magnified 350 diameters (Kölliker). *a*, natural state; *b*, treated with acetic acid.

or wrinkles when the artery contracts. This latter membrane, the striated or fenestrated coat of Henle, is peculiar in its tendency to curl up, when peeled off from the artery, and in the perforated and streaked appearance which it presents under the microscope. Its inner surface is lined with a delicate layer of epithelium, composed of thin squamous elongated cells, which make it smooth and polished, and furnish a nearly impermeable surface, along which the blood may flow with the smallest possible amount of resistance from friction.

Fig. 41.*

The walls of the arteries, with the possible exception of the epithelial lining and the layers of the internal coat immediately outside it, are not nourished by the blood which they convey, but are, like other parts of the body, supplied with little arteries, ending in capillaries and veins, which, branching throughout the external coat, extend for some distance into the middle, but do not reach the internal coat. These nutrient vessels are called *vasa vasorum*. Nerve-fibres are also supplied to the walls of the arteries.

The function of the arteries is to convey blood from the heart to all parts of the body, and each tissue which enters into the construction of an artery has a special purpose to serve in this distribution.

(1.) The external coat forms a strong and tough investment, which, though capable of extension, appears principally designed to strengthen the arteries and to guard against their excessive distension from the force of the

* Fig. 41. Portion of fenestrated membrane from the crural artery, magnified 200 diameters. *a*, *b*, *c*, perforations (from Henle).

heart's action. In it, too, the little *vasa vasorum* find a suitable tissue in which to subdivide for the supply of the arterial coats.

(2.) The purpose of the elastic tissue, which enters so largely into the formation of all the coats of the arteries, is, *1st.* To guard the arteries from the suddenly exerted pressure to which they are subjected at each contraction of the ventricles. In every such contraction, the contents of the ventricles are forced into the arteries more quickly than they can be discharged into and through the capillaries. The blood therefore being, for an instant, resisted in its onward course, a part of the force with which it was impelled is directed against the sides of the arteries; under this force, which might burst a brittle tube, their elastic walls dilate, stretching enough to receive the blood, and as they stretch, becoming more tense and more resisting. Thus, by yielding, they, as it were, break the shock of the force impelling the blood, and exhaust it before they are in danger of bursting, through being overstretched. Elasticity is thus advantageous in all arteries, but chiefly so in the aorta and its large branches, which are provided, as already said, with a large proportional quantity of elastic tissue, in adaptation to the great force of the left ventricle, which falls first on them, and to the increased pressure of the arterial blood in violent expiratory efforts.

On the subsidence of the pressure, when the ventricles cease contracting, the arteries are able, by the same elasticity, to resume their former calibre; and in thus doing, they manifest the *2nd* chief purpose of their elasticity, that, namely, of equalizing the current of the blood by maintaining pressure on the blood in the arteries during the periods at which the ventricles are at rest or dilating. If some such method as this had not been adopted—if for example the arteries had been rigid tubes, the blood, instead of flowing as it does, in a constant stream, would have been propelled through the arterial system in a series

of jerks corresponding to the ventricular contractions, with intervals of almost complete rest during the inaction of the ventricles. But in the actual condition of the arteries, the force of the successive contractions of the ventricles is expended partly in the direct propulsion of the blood, and partly in the dilatation of the elastic arteries; and in the intervals between the contractions of the ventricles, the force of the recoiling and contracting arteries is employed in continuing the same direct propulsion. Of course, the pressure exercised by the recoiling arteries is equally diffused in every direction through the blood, and the blood would tend to move backwards as well as onwards, but that all movement backwards is prevented by the closure of the semi-lunar arterial valves, which takes place at the very commencement of the recoil of the arterial walls.

By this exercise of the elasticity of the arteries, all the force of the ventricles is made advantageous to the circulation; for that part of their force which is expended in dilating the arteries, is restored in full, according to that law of action of elastic bodies, by which they return to the state of rest with a force equal to that by which they were disturbed therefrom. There is thus no loss of force; but neither is there any gain, for the elastic walls of the artery cannot originate any force for the propulsion of the blood—they only restore that which they received from the ventricles; they would not contract had they not first been dilated, any more than a spiral spring would shorten itself unless it were first elongated. The advantage of elasticity in this respect is, therefore, not that it increases, but that it equalizes or diffuses the force derived from the periodic contractions of the ventricles. The force with which the arteries are dilated every time the ventricles contract, might be said to be received by them in store, to be all given out again in the next succeeding period of dilatation of the ventricles. It is by this equalizing influence of the

successive branches of every artery that, at length, the intermittent accelerations produced in the arterial current by the action of the heart, cease to be observable, and the jetting stream is converted into the continuous and equable movement of the blood which we see in the capillaries and veins.

In the production of a continuous stream of blood in the smaller arteries and capillaries, the resistance which is offered to the blood-stream in the capillaries (p. 161), is a necessary agent. Were there no greater obstacle to the *escape* of blood from the arteries than exists to its *entrance* into them from the heart, the stream would be intermittent, notwithstanding the elasticity of the walls of the arteries.

It is the resistance which the left ventricle meets with in forcing blood into the arteries that causes part of the force of its contraction to be expended in dilating them, or, as before remarked, in laying up in them a power which will act in the intervals of the ventricle's contraction.

(3.) By means of the elastic tissue in their walls (and of the muscular tissue also), the arteries are enabled to dilate and contract readily in correspondence with any temporary increase or diminution of the total quantity of blood in the body; and within a certain range of diminution of the quantity, still to exercise due pressure on their contents.

The elastic coat, however, not only assists in restoring the normal calibre of an artery after temporary *dilatation*, but also, (4) may assist in restoring it after *dimin utio* of the calibre, whether this be caused by a temporary contraction of the muscular coat, or the application of a compressing force from without. This action of the elastic tissue in arteries, is well shown in arteries which contract after death, but regain their average patency on the cessation of post-mortem rigidity (p. 140). (5.) By means of their elastic coat the arteries are enabled to adapt them-

selves to the different movements of the several parts of the body.

We have already referred to the fact that the middle coat of the arteries is composed of unstriped muscular fibres, mingled with fine elastic filaments. The evidence for the muscular *contractility* of arteries may, however, be given briefly for the sake of the physiological facts on which it hinges.

(1.) When a small artery in the living subject is exposed to the air or cold, it gradually but manifestly contracts. Hunter observed that the posterior tibial artery of a dog when laid bare, became in a short time so much contracted as almost to prevent the transmission of blood; and the observation has been often and variously confirmed. Simple elasticity could not effect this; for after death, when the vital muscular power has ceased, and the mechanical elastic one alone operates, the contracted artery dilates again.

(2.) When an artery is cut across, its divided ends contract, and the orifices may be completely closed. The rapidity and completeness of this contraction vary in different animals; they are generally greater in young than in old animals; and less, apparently, in man than in animals. In part this contraction is due to elasticity, but in part, no doubt, to muscular action; for it is generally increased by the application of cold, or of any simple stimulating substances, or by mechanically irritating the cut ends of the artery, as by picking or twisting them. Such irritation would not be followed by these effects, if the arteries had no other power of contracting than that depending upon elasticity.

(3.) The contractile property of arteries continues many hours after death, and thus affords an opportunity of distinguishing it from elasticity. When a portion of an artery, the splenic, for example, of a recently killed animal, is exposed, it gradually contracts, and its canal may be

thus completely closed: in this contracted state it remains for a time, varying from a few hours to two days: then it dilates again, and permanently retains the same size. If, while contracted, the artery be forcibly distended, its contractility is destroyed, and it holds a middle or natural size.

This persistence of the contractile property after death was well shown in an observation of Hunter, which may be mentioned as proving, also, the greater degree of contractility possessed by the smaller than by the larger arteries. Having injected the uterus of a cow, which had been removed from the animal upwards of twenty-four hours, he found, after the lapse of another day, that the larger vessels had become much more turgid than when he injected them, and that the smaller arteries had contracted so as to force the injection back into the larger ones.

The results of an experiment which Hunter made with the vessels of an umbilical cord prove still more strikingly the long continuance of the contractile power of arteries after death. In a woman delivered on a Thursday afternoon, the umbilical cord was separated from the fœtus, having been first tied in two places, and then cut between, so that the blood contained in the cord and placenta was confined in them. On the following morning, Hunter tied a string round the cord, about an inch below the other ligature, that the blood might still be confined in the placenta and remaining cord. Having cut off this piece, and allowed all the blood to escape from its vessels, he attentively observed to what size the ends of the cut arteries were brought by the elasticity of their coats, and then laid aside the piece of cord to see the influence of the contractile power of its vessels. On Saturday morning, the day after, the mouths of the arteries were completely closed up. He repeated the experiment the same day with another portion of the same cord, and on the following morning found the results to be precisely similar. On the Sunday, he performed the experiment the third time, but

the artery then seemed to have lost its contractility, for on the Monday morning, the mouths of the cut arteries were found open. In each of these experiments there was but little alteration perceived in the orifices of the veins.

(4.) The influence of cold in increasing the contraction of a divided artery has been referred to: it has been shown, also, by Schwann, in an experiment on the mesentery of a living toad. Having extended the mesenter under the microscope, he placed upon it a few drops of water, the temperature of which was some degrees lower than that of the atmosphere. The contraction of the vessels soon commenced, and gradually increased until, at the expiration of ten or fifteen minutes, the diameter of the canal of an artery, which at first was 0·0724 of an English line, was reduced to 0·0276. The arteries then dilated again, and at the expiration of half an hour had acquired nearly their original size. By renewing the application of the water, the contraction was reproduced: in this way the experiment could be performed several times on the same artery. It is thus proved, that cold will excite contraction in the walls of very small, as well as of comparatively large arteries: it could not produce such contraction in a merely elastic substance; but it is a stimulus to the organic muscular fibres in many other parts, as well as in the arterial coat; as, *e.g.*, in the skin, the dartos, and the walls of the bronchi.

(5.) Lastly, satisfactory evidence of the muscularity of the arterial coats is furnished by the experiments of Ed. and E. H. Weber, and of Professor Kölliker, in which they applied the stimulus of electro-magnetism to small arteries. The experiments of the Webers were performed on the small mesenteric arteries of frogs; and the most striking results were obtained when the diameter of the vessels examined did not exceed from $\frac{1}{7}$ to $\frac{1}{17}$ of a Paris line. When a vessel of this size was exposed to the electric current, its diameter in from five to ten seconds, became

one-third less, and the area of its section about one-half. On continuing the stimulus, the narrowing gradually increased, until the calibre of the tube became from three to six times smaller than it was at first, so that only a single row of blood-corpuscles could pass along it at once; and eventually the vessel was closed and the current of blood arrested.

With regard to the *purpose served by the muscular coat* of the arteries, there appears no sufficient reason for supposing that it assists, to more than a very small degree, in propelling the onward current of blood. Its most important office is that of regulating the quantity of blood to be received by each part, and of adjusting it to the requirements of each, according to various circumstances, but chiefly and most naturally, according to the activity with which the functions of each part are at different times performed. The amount of work done by each organ of the body varies at different times, and the variations often quickly succeed each other, so that, as in the brain for example, during sleep and waking, within the same hour a part may be now very active and then inactive. In all its active exercise of function, such a part requires a larger supply of blood than is sufficient for it during the times when it is comparatively inactive. It is evident that the heart cannot regulate the supply to each part at different periods, neither could this be regulated by any general and uniform contraction of the arteries; but it may be regulated by the power which the arteries of each part have, in their muscular tissue, of contracting so as to diminish, and of passively dilating or yielding so as to permit an increase of, the supply of blood, according as the requirements of the part may demand. And thus, while the ventricles of the heart determine the total quantity of blood, to be sent onwards at each contraction, and the force of its propulsion, and while the large and merely elastic arteries distribute it and equalise its stream,

the smaller arteries with muscular tissue add to these two purposes, that of regulating and determining, according to its requirements, the proportion of the whole quantity of blood which shall be distributed to each part.

It must be remembered, however, that this regulating function of the arteries is itself governed and directed by the nervous system.

The muscular tissue of arteries is supplied with nerves chiefly, if not entirely, by branches from the sympathetic system. These so-called *vaso-motor* nerves are again connected, through the medium of ganglia, with the fibres from the sympathetic system supplied to the organs nourished by these same arteries. Thus, any condition in these organs which causes them to need a different amount of blood, whether more or less, produces a certain impression on their nerves, and by these the impression is carried to the ganglia, and thence reflected along the nerves which supply the arteries. The muscular element of these vessels responds in obedience to the impression conveyed to it by the nerves; and, according to its contraction or dilatation, is a larger or smaller quantity of blood allowed to pass.

Another function of the muscular element of the middle coat of arteries is, doubtless, to co-operate with the elastic in adapting the calibre of the vessels to the quantity of blood which they contain. For the amount of fluid in the blood-vessels varies very considerably even from hour to hour, and can never be quite constant; and were the elastic tissue only present, the pressure exercised by the walls of the containing vessels on the contained blood would be sometimes very small, and sometimes inordinately great. The presence of a muscular element, however, provides for a certain uniformity in the amount of pressure exercised; and it is by this adaptive, uniform, gentle, muscular contraction, that the *tone* of the blood-vessels is maintained. Deficiency of this *tone* is the cause of the soft and yield-

ing pulse, and its unnatural excess of the hard and tense one.

The elastic and muscular contraction of an artery may also be regarded as fulfilling a natural purpose when, the artery being cut, it first limits and then, in conjunction with the coagulated fibrin, arrests the escape of blood. It is only in consequence of such contraction and coagulation that we are free from danger through even very slight wounds; for it is only when the artery is closed that the processes for the more permanent and secure prevention of bleeding are established.

Mr. Savory has shown that the natural state of all arteries, in regard at least to their length, is one of tension—that they are always more or less stretched, and ever ready to recoil by virtue of their elasticity, whenever the opposing force is removed. The extent to which the divided extremities of arteries retract is a measure of this tension, not of their elasticity.

From what has been said in the preceding pages, it appears that the office of the arteries in the circulation is,—1*st*, the conveyance and distribution of blood to the several parts of the body; 2*nd*, the equalization of the current, and the conversion of the pulsatile jetting movement given to the blood by the ventricles, into an uniform flow; 3*rd*, the regulation of the supply of blood to each part, in accordance with its demands.

The Pulse.

The jetting movement of the blood, which, as just stated, it is one of the offices of the arteries to change into an uniform motion, is the cause of *the pulse*, and therefore needs a separate consideration. We have already said, that as the blood is not able to pass through the arteries so quickly as it is forced into them by the ventricle, on account of the resistance it experiences in the capillaries, a part of the

force with which the heart impels the blood is exercised upon the walls of the vessels which it distends. The distension of each artery increases both its length and its diameter. In their elongation, the arteries change their form, the straight ones becoming curved, or having such a tendency, and those already curved becoming more so;* but they recover their previous form as well as their diameter when the ventricular contraction ceases, and their elastic walls recoil. The increase of their curves which accompanies the distension of arteries, and the succeeding recoil, may be well seen in the prominent temporal artery of an old person. The elongation of the artery is in such a case quite manifest.

The dilatation or increase of the diameter of the artery is less evident. In several reptiles, it may be seen without aid, in the immediate vicinity of the heart, and it may be watched, with a simple magnifying glass, in the aorta of the tadpole. Its slight amount in the smaller arteries, the difficulty of observing it in opaque parts, and the rapidity with which it takes place, are sufficient to account for its being, in Mammalia, imperceptible to the eye. But in these also experiment has proved its occurrence. Flourens, in evidence of such dilatation, says he encircled a large artery with a thin elastic metallic ring cleft at one point, and that at the moment of pulsation the cleft part became perceptibly widened.

This dilatation of an artery, and the elongation producing curvature, or increasing the natural curves, are sensible to the finger placed over the vessel, and produce the pulse. The mind cannot distinguish the sensation produced by the dilatation from that produced by the elongation and

* There is, perhaps, an exception to this in the case of the aorta, of which the curve is by some supposed to be diminished when it is elongated; but if this be so, it is because only one end of the arch is immoveable; the other end, with the heart, may move forward slightly when the ventricles contract.

curving; that which it perceives most plainly, however, is the dilatation.*

The pulse—due to any given beat of the heart—is not perceptible at the same moment in all the arteries of the body. Thus it can be felt in the carotid a very short time before it is perceptible in the radial artery, and in this vessel again before the dorsal artery of the foot. The delay in the beat is in proportion to the distance of the artery from the heart, but the difference in time between

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* For this fact, which is contrary to the commonly accepted doctrine, I am indebted to my friend, Dr. Hensley, who has kindly furnished me with the following note on the subject:—

By determining the conditions of equilibrium of a portion of artery supposed cylindrical and filled with blood at a given pressure, it is easily shown that the transverse tension is double the longitudinal.

Also it may be shown experimentally that, if strips of equal breadth, cut in the two directions from one of the larger arteries, be stretched by equal weights, the stretching of the transverse slip is somewhat greater than that of the longitudinal one.

(*By the word stretching is to be understood amount of stretching, and not increase of length:—it may be measured by the ratio which the increase of length bears to the original length:—Thus things whose natural lengths are* 5 *and* 10 *inches are equally stretched when their lengths are made* 6 *and* 12 *inches respectively.*)

Such experiments also show that, within certain limits, the stretching of each strip varies directly as its tension.

Hence it will be seen that the transverse stretching of an artery, when filled with blood, must be somewhat more than double its longitudinal stretching.

This being true for different blood pressures, the difference between the *transverse* stretchings for different pressures must be somewhat more than double the difference between the corresponding *longitudinal* stretchings; and thus we can hardly be justified in saying that the increase of longitudinal stretching which takes place with the pulse is greater than the increase of transverse stretching.

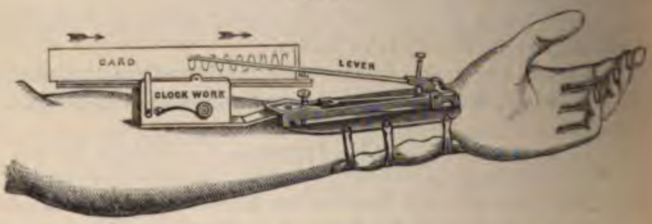
It must also be remembered that the arteries are, under all circumstances, naturally in a state of tension longitudinally, and that their length, therefore, cannot be increased at all until the blood pressure is increased beyond a certain point.—(Ed.)

the beat of any two arteries never exceeds probably $\frac{1}{6}$ to $\frac{1}{8}$ of a second.

A great deal of light has been thrown on what may be called the form of the pulse by the sphygmograph (figs. 42 and 43). The principle on which the sphygmograph acts is very simple (see fig. 42). The small button replaces the finger in the ordinary act of taking the pulse, and is made to rest lightly on the artery, the pulsations of which it is desired to investigate. The up-and-down movement of the button is communicated to the lever, to the hinder end of which is attached a slight spring, which allows the lever to move up, at the same time that it is

Fig. 42.*

Fig. 43.†



just strong enough to resist its making any sudden jerk, and in the interval of the beats also to assist in bringing it

* Fig. 42. Diagram of the mode of action of the Sphygmograph.
† Fig. 43. The Sphygmograph applied to the arm.

back to its original position. For ordinary purposes, the instrument is bound on the wrist (fig. 43).

It is evident that the beating of the pulse with the reaction of the spring will cause an up-and-down movement of the lever, and if the extremity of the latter be inked, it will write the effect on the card, which is made to move by clockwork in the direction of the arrow. Thus a tracing of the pulse is obtained, and in this way much more delicate effects can be seen, than can be felt on the application of the finger.

Fig. 44 represents a healthy pulse-tracing of the radial artery, but somewhat deficient in *tone*. On examination, we see that the up-stroke which represents the beat of the pulse is a nearly vertical line, while the down-stroke is

Fig. 44.*

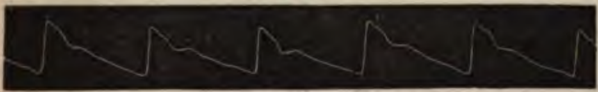


Fig. 45.†

Fig. 46.‡

very slanting, and interrupted by a slight re-ascent. The more vigorous the pulse, if it be healthy, the less is this re-ascent, and *vice versâ*. Fig. 45 represents the tracing

* Fig. 44. Pulse-tracing of radial artery, somewhat deficient in *tone*.
† Fig. 45. Firm and long pulse of vigorous health.
‡ Fig. 46. Pulse-tracing of radial artery, with double apex.
The above tracings are taken from Dr. Sanderson's work "On the Sphygmograph."

of a healthy pulse in which the tone of the vessel is better than in the last instance, and the down-stroke is therefore less interrupted.

Sometimes the up-stroke has a double apex, as in fig. 46. This will be explained hereafter.

Before proceeding to consider the formation of the pulse, as shown by these tracings, it is necessary to consider what are the elements combined to produce it.

The heart at regular intervals discharges a certain quantity of blood into the arteries and their branches, already filled, though not distended to the utmost, with fluid. This fresh quantity of blood obtains entrance by the yielding of the artery's elastic walls, and, on the cessation of the propelling force, and when these walls recoil, the blood is prevented from returning into the ventricle whence it is issued, by the shutting of the semi-lunar valves in the manner before described (p. 117). The pressure, therefore, which is exercised on the blood by the contracting arterial walls, will cause it to travel in a direction away from the heart, or, in other words, towards the capillaries and veins.

It was formerly supposed that the pulse was caused not by the direct action of the ventricle, but by the propagation of a wave in consequence of the elastic recoil of the large arteries, after their distension; and successive acts of dilatation and recoil, extending along the arteries in the direction of the circulation, were supposed to account for the later appearance of the pulse in the vessels most distant from the heart. The fact, however, that the pulse is perceptible in every part of the arterial system previous to the occurrence of the second sound of the heart, that is, previous to the closure of the aortic valves, is a fatal objection to this theory. For, if the pulse were the effect of a wave propagated by the alternate dilatation and contraction of successive portions of the arterial tube, it ought, in all the arteries except those nearest to the heart, to

follow or coincide with, but could never precede, the second sound of the heart; for the first effect of the elastic recoil of the arteries first dilated is the closure of the aortic valves; and their closure produces the second sound.

The theory which seems to reconcile all the facts of the case, and especially those two which appear most opposed, namely, that the pulse always precedes the second sound of the heart, and yet is later in the arteries far from the heart than in those near it, may be thus stated:—It supposes that the blood which is impelled onwards by the left ventricle does not so impart its pressure to that which the arteries already contain, as to dilate the whole arterial system at once; but that it enters the arteries, it displaces and propels that which they before contained, and flows on with what may be called a *head-wave*, like that which is formed when a rapid stream of water overtakes another moving more slowly. The slower stream offers resistance to the more rapid one, till their velocities are equalized: and, because of such resistance, some of the force of the more rapid stream of blood just expelled from the ventricle, is diverted laterally, and with the rising of the wave the arteries nearest the heart are dilated and elongated. They do not at once recoil, but continue to be distended so long as blood is entering them from the ventricle. The wave at the head of the more rapid stream of blood runs on, propelled and maintained in its velocity by the continuous contraction of the ventricle: and it thus dilates in succession every portion of the arterial system, and produces the pulse in all. At length, the whole arterial system (wherein a pulse can be felt) is dilated; and at this time, when the wave we have supposed has reached all the smaller arteries, the entire system may be said to be simultaneously dilated; then it begins to contract, and the contractions of its several parts ensue in the same succession as the dilatations, commencing at the heart. The contraction of the first portion produces the closure of the valves

and the second sound of the heart; and both it and the progressive contractions of all the more distant parts maintain, as already said, that pressure on the blood during the inaction of the ventricle, by which the stream of the arterial blood is sustained between the jets, and is finally equalized by the time it reaches the capillaries.

It may seem an objection to this theory, that it would probably require a larger quantity of blood to dilate all the arteries than can be discharged by the ventricle at each contraction. But the quantity necessary for such a purpose is less than might be supposed. Injections of the arteries prove that, including all down to those of about one-eighth of a line in diameter, they do not contain on an average more than one and a half pints of fluid, even when distended. There can be no doubt, therefore, that the three or four ounces which the ventricle is supposed to discharge at each contraction, being added to that which already fills the arteries, would be sufficient to distend them all.

A distinction must be carefully made between the passage of the *wave* along the arteries, and the velocity of the *stream* (p. 155) of blood. Both wave and current are present; but the rates at which they travel are very different, that of the wave being twenty or thirty times as great as that of the current.

Returning now to the consideration of the pulse-tracings (p. 147), it may be remarked that, in each, the up-stroke corresponds with the period during which the ventricle is contracting; the down-stroke, with the interval between its contractions, or in other words with the recoil, after distension, of the elastic arteries. In the large arteries, when at least there is much loss of *tone*, the up-stroke is double, as in fig. 46, the almost instantaneous propagation of the force of contraction of the left ventricle along the column of blood in the arteries, or the percussion-impulse, as it is termed by Dr. Sanderson, being sufficiently strong

to jerk up the lever for an instant, while the *wave* of blood, rather more slowly propagated from the ventricle, catches it, so to speak, as it begins to fall, and again slightly raises it.

In the radial artery tracings, on the other hand, we see that the up-stroke is single. In this case the percussion-impulse is not sufficiently strong to jerk up the lever and produce an effect distinct from that of the systolic *wave* which immediately follows it, and which continues and completes the distension. In cases of feeble arterial tension, however, the percussion-impulse may be traced by the sphygmograph, not only in the carotid pulse, but to a less extent in the radial also.

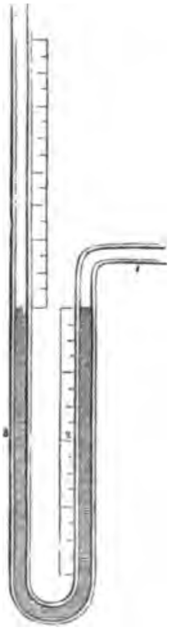
In looking now at the down-stroke (fig. 44) in the tracings, we see that in the case of an artery with deficient *tone*, it is interrupted by a well-marked notch, or, in other words, that the descent is interrupted by a slight uprising. There are indications also of slighter irregularities or vibrations during the fall of the lever; while these are alone to be seen in the pulse of health, or, in other words, when the walls of the artery are of good tone (fig. 45). In some cases of disease the re-ascent is so considerable as to be perceptible to the finger, and this double beat has received the technical name of "dicrotous" pulse. As a diseased condition this has long been recognized, but it is only since the invention of the sphygmograph that it has been found to belong in a certain degree to the normal pulse also.

Various theories have been framed to account for the dicrotism of the pulse. By some, it is supposed to be due to the aortic valves, the sudden closure of which stops the incipient regurgitation of blood into the ventricle, and causes a momentary rebound throughout the arterial system; while Dr. Sanderson considers it to be caused by a kind of rebound from the periphery rather than from the central part of the circulating apparatus.

Force of the Blood in the Arteries.

The force with which the ventricles act in their contraction, and the reasons for believing it sufficient for the circulation of the blood, have been already mentioned. Both calculation and experiment have proved, that very little of this force is consumed in the arteries. Dr. Thomas

Fig. 47.



Young calculated that the loss of force in overcoming friction and other hindrances in the arteries would be so slight, that if one tube were introduced into the aorta, and another into any other artery, even into one as fine as hair, the blood would rise in the tube from the small vessel to within two inches of the height to which it would rise from the large vessel. The correctness of the calculation is established by the experiments of Poiseuille, who invented an instrument named a hæmadynamometer, for estimating the statical pressure exercised by the blood upon the walls of the arteries. It consists of a long glass tube, bent so as to have a short horizontal portion (fig. 47), a branch (2) descending at right angles from it, and a long ascending branch (3). Mercury poured into the ascending and descending portions, will necessarily have the same level in both branches, and in a vertical position the height of its column must be the same in both. If, now, the blood is made to flow from an artery, through the horizontal portion of the tube (which should contain a solution of carbonate of potash to prevent coagulation) into the descending branch, it will exert on the mercury a

pressure equal to the force by which it is moved in the arteries; and the mercury will, in consequence, descend in this branch, and ascend in the other. The depth to which it sinks in the one branch, added to the height to which it rises in the other, will give the whole height of the column of mercury which balances the pressure exerted by the blood; the weight of the blood, which takes the place of the mercury in the descending branch, and which is more than ten times less than the same quantity of quicksilver, being subtracted. Poiseuille thus calculated the force with which the blood moves in an artery, according to the laws of hydrostatics, from the diameter of the artery, and the height of the column of quicksilver; that is to say, from the weight of a column of mercury, whose base is a circle of the same diameter as the artery, and whose height is equal to the difference in the levels of the mercury in the two branches of the instrument. He found the blood's pressure equal in all the arteries examined; difference in size, and distance from the heart being unattended by any corresponding difference of force in the circulation. The height of the column of mercury displaced by the blood was the same in all the arteries of the same animal. The correctness of these views having been questioned, Poiseuille has recently repeated his observations, and obtained the same results.

From the mean result of several observations on horses and dogs, he calculated that the force with which the blood is moved in any large artery, is capable of supporting a column of mercury six inches and one and a half lines in height, or a column of water seven feet one line in height. With these results, the more recent observations of other experimenters closely accord. Poiseuille's experiments having thus shown to him that the force of the blood's motion is the same in the most different arteries, he concluded that, to measure the amount of the blood's pressure in any artery of which the calibre is known, it is

necessary merely to multiply the area of a transverse section of a vessel by the height of the column of mercury which is already known to be supported by the force of the blood in any part of the arterial system. The weight of a column of mercury of the dimensions thus found, will represent the pressure exerted by the column of blood. And assuming that the mean of the greatest and least height of the column of mercury found, by experiments on different animals, to be supported by the force of the blood in them, is equivalent to the height of the column which the force of the blood in the human aorta would support, he calculated that about 4 lbs. 4 oz. avoirdupois would indicate the static force with which the blood is impelled into the human aorta. By the same calculation, he estimated the force of the circulation in the aorta of the mare to be about 11 lbs. 9 oz. avoirdupois: and that in the radial artery at the human wrist only 4 drs. We have already seen that the muscular force of the right ventricle is equal to only one half that of the left, consequently, if Poiseuille's estimate of the latter be correct, the force with which the blood is propelled into the lungs will only be equal to 2 lbs. 2 oz. avoirdupois.

The amounts above stated indicate the pressure exerted by the blood at the several parts of the arterial system at the time of the ventricular contraction. During the dilatation, this pressure is somewhat diminished. Hales observed, that the column of blood in the tube inserted into an artery, falls an inch, or rather more, after each pulse; Ludwig has observed the same, and recorded it more minutely. The pressure is also influenced by the various circumstances which affect the action of the heart; the diminution or increase of the pressure being proportioned to the weaker or stronger action of this organ. Valentin observed that, on increasing the amount of blood by the injection of a fresh quantity into it, the pressure in the vessels was also increased, while a

contrary effect ensued on diminishing the quantity of blood.

Velocity of the Blood in the Arteries.

The velocity of the stream of blood is greater in the arteries than in any other part of the circulatory system, and in them it is greatest in the neighbourhood of the heart, and during the ventricular systole; the rate of movement diminishing during the diastole of the ventricles, and in the parts of the arterial system most distant from the heart. From Volkmann's experiments with the hæmodromometer, it may be concluded that the blood moves in the large arteries near the heart at the rate of about ten or twelve inches per second. Vierordt calculated the rapidity of the stream at about the same rate in the arteries near the heart, and at two and a quarter inches per second in the arteries of the foot.

THE CAPILLARIES.

In all organic textures, except some parts of the corpora cavernosa of the penis, and of the uterine placenta, and of the spleen, the transmission of the blood from the minute branches of the arteries to the minute veins is effected through a network of microscopic vessels, in the meshes of which the proper substance of the tissue lies (fig. 48). This may be seen in all minutely injected preparations; and during life, by the aid of the microscope, in any transparent vascular parts,—such as the web of the frog's foot, the tail or external branchiæ of the tadpole, or the wing of the bat.

The ramifications of the minute arteries form repeated anastomoses with each other and give off the capillaries which, by their anastomoses, compose a continuous and uniform network, from which the venous radicles, on the other hand, take their rise. The reticulated vessels connecting the arteries and veins are called capillary, on ac-

count of their minute size; and intermediate vessels, on account of their position. The point at which the arteries terminate and the minute veins commence, cannot be exactly defined, for the transition is gradual; but the intermediate network has, nevertheless, this peculiarity, that the small vessels which compose it maintain the same diameter throughout; they do not diminish in diameter in one direction, like arteries and veins; and the meshes of the network that they compose are more uniform in shape and size than those formed by the anastomoses of the minute arteries and veins.

Fig. 48.*

The structure of the capillaries is much more simple than that of the arteries or veins. Their walls are composed of a single layer of elongated or radiate, flattened and nucleated cells, so joined and dovetailed together as to form a continuous transparent membrane (fig. 49). Outside these cells, in the larger capillaries, there is a structureless, or very finely fibrillated membrane, on the inner surface of which they are laid down.

The *diameter* of the capillary vessels varies somewhat in the different textures of the body, the most common size being about $\frac{1}{3000}$th of an inch. Among the smallest may be mentioned those of the brain, and of the follicles of the mucous membrane of the intestines; among the

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* Fig. 48. Blood-vessels of an intestinal villus, representing the arrangement of capillaries between the ultimate venous and arterial branches; *a*, *a*, the arteries; *b*, the vein.

arrangement, a single capillary projecting from the common network into some prominent organ, and returning after forming one or more loops, as in the papillæ of the tongue and skin. Whatever be the form of the capillary network in any tissue or organ, it is, as a rule, found to prevail in the corresponding parts of all animals.

The *number* of the capillaries and the *size of the meshes* in different parts determine in general the degree of *vascularity* of those parts. The parts in which the network of capillaries is closest, that is, in which the meshes or interspaces are the smallest, are the lungs and the choroid membrane of the eye. In the iris and ciliary body the interspaces are somewhat wider, yet very small. In the human liver, the interspaces are of the same size, or even smaller than the capillary vessels themselves. In the human lung they are smaller than the vessels; in the human kidney, and in the kidney of the dog, the diameter of the injected capillaries, compared with that of the interspaces, is in the proportion of one to four, or of one to three. The brain receives a very large quantity of blood; but the capillaries in which the blood is distributed through its substance are very minute, and less numerous than in some other parts. Their diameter, according to E. H. Weber, compared with the long diameter of the meshes, being in the proportion of one to eight or ten; compared with the transverse diameter, in the proportion of one to four or six. In the mucous membranes—for example, in the conjunctiva—and in the cutis vera, the capillary vessels are much larger than in the brain, and the interspaces narrower,—namely, not more than three or four times wider than the vessels. In the periosteum the meshes are much larger. In the cellular coat of arteries, the width of the meshes is ten times that of the vessels (Henle).

It may be held as a general rule, that the more active the functions of an organ are, the more vascular it is; that is, the closer is its capillary network and the larger its

supply of blood. Hence the narrowness of the interspaces in all glandular organs, in mucous membranes, and in growing parts; their much greater width in bones, ligaments, and other very tough and comparatively inactive tissues; and the complete absence of vessels in cartilage, the dense tendons of adults, and such parts as those in which, probably, very little organic change occurs after they are once formed. But the general rule must be modified by the consideration, that some organs, such as the brain, though they have small and not very closely arranged capillaries, may receive large supplies of blood by reason of its more rapid movement. When an organ has large arterial trunks and a comparatively small supply of capillaries, the movement of the blood through it will be so quick, that it may, in a given time, receive as much fresh blood as a more vascular part with smaller trunks, though at any given instant the less vascular part will have in it a smaller quantity of blood.

In the Circulation in the Capillaries, as seen in any transparent part of a living adult animal by means of the microscope (fig. 52), the blood flows with a constant equable motion. In very young animals, the motion, though continuous, is accelerated at intervals corresponding to the pulse in the larger arteries, and a similar motion of the blood is also seen in the capillaries of adult animals when they are feeble: if their exhaustion is so great that the power of the heart is still more diminished, the red corpuscles are observed to have merely the periodic motion,

Fig. 52.*

* Fig. 52. Capillaries in the web of the frog's foot magnified.

and to remain stationary in the intervals; while, if the debility of the animal is extreme, they even recede somewhat after each impulse, apparently because of the elasticity of the capillaries, and the tissues around them. These observations may be added to those already advanced (p. 132) to prove that, even in the state of great debility, the action of the heart is sufficient to impel the blood through the capillary vessels. Moreover, Dr. Marshall Hall having placed the pectoral fin of an eel in the field of the microscope and compressed it by the weight of a heavy probe, observed that the movement of the blood in the capillaries became obviously pulsatory, the pulsations being synchronous with the contractions of the ventricle. The pulsatory motion of the blood in the capillaries cannot be attributed to an action in these vessels; for, when the animal is tranquil, they present not the slightest change in their diameter.

It is in the capillaries, that the chief resistance is offered to the progress of the blood; for in them the friction of the blood is greatly increased by the enormous multiplication of the surface with which it is brought in contact. The velocity of the blood is also in them reduced to its minimum, because of the widening of the stream. If, as Professor Müller says, the sectional area of all the branches of a vessel united were always the same as that of the vessel from which they arise, and if the aggregate sectional area of the capillary vessels were equal to that of the aorta, the mean rapidity of the blood's motion in the capillaries would be the same as in the aorta and largest arteries; and if a similar correspondence of capacity existed in the veins and arteries, there would be an equal correspondence in the rapidity of the circulation in them. It is quite true, that the force with which the blood is propelled in the arteries, as shown by the quantity of blood which escapes from them in a certain space of time, is greater than that with which it moves in the veins;

but this force has to overcome all the resistance offered in the arterial and capillary system—the heart itself, indeed, must overcome this resistance; so that the excess of the force of the blood's motion in the arteries is expended in overcoming this resistance, and the rapidity of the circulation in the arteries, even from the commencement of the aorta, would be the same as in the veins and capillaries, if the aggregate capacity of each of the three systems of vessels were the same.

But since the aggregate sectional area of the branches is greater than that of the trunk from which they arise, the rapidity of the blood's motion will necessarily be greater in the trunk, and will diminish in proportion as the aggregate capacity of the vessels increases during their ramification: in the same manner as, other things being equal, the velocity of a stream diminishes as it widens.

The observations of Hales, E. H. Weber, and Valentin, agree very closely as to the rate of the blood in the capillaries of the frog: and the mean of their estimates gives the velocity of the systemic capillary circulation at about one inch per minute. Through the pulmonic capillaries, the rate of motion, according to Hales, is about five times that through the systemic ones. The velocity in the capillaries of warm-blooded animals is greater, but has not yet been accurately estimated. If it be assumed to be three times as great as in the frog, still the estimate may seem too low, and inconsistent with the facts, which show that the whole circulation is accomplished in about a minute. But the whole length of capillary vessels, through which any given portion of blood has to pass, probably does not exceed $\frac{1}{30}$th of an inch; and therefore the time required for each quantity of blood to traverse its own appointed portion of the general capillary system will scarcely amount to a second: while in the pulmonic capillary system the length of time required will be much less even than this.

The estimates given above are drawn from observations of the movements of the red blood-corpuscles, which move in the centre of the stream. At the circumference of the stream, in contact with the walls of the vessel, and adhering to them, there is a layer of liquor sanguinis which appears to be motionless. The existence of this *still layer*, as it is termed, is inferred both from the general fact that such an one exists in all fine tubes traversed by fluid, and from what can be seen in watching the movements of the blood-corpuscles. The red corpuscles occupy the middle of the stream and move with comparative rapidity; the colourless lymph-corpuscles run much more slowly by the walls of the vessel; while next to the wall there is often a transparent space in which the fluid appears to be at rest; for if any of the corpuscles happen to be forced within it, they move more slowly than before, rolling lazily along the side of the vessel, and often adhering to its wall. Part of this slow movement of the pale corpuscles and their occasional stoppage may be due, as E. H. Weber has suggested, to their having a natural tendency to adhere to the walls of the vessels. Sometimes, indeed, when the motion of the blood is not strong, many of the white corpuscles collect in a capillary vessel, and for a time entirely prevent the passage of the red corpuscles. But there is no doubt that such a still layer of liquor sanguinis exists next the walls of the vessels, and it is between this and the tissues around the vessels that those interchanges of particles take place which ensue in nutrition, secretion, and absorption by the blood-vessels; interchanges which are probably facilitated by the tranquillity of the fluids between which they are effected.

Until within the last few years it has been generally supposed that the occurrence of any transudation from the interior of the capillaries into the midst of the surrounding tissues was confined, in the absence of injury, strictly to the fluid part of the blood; in other words, that the corpuscles

could not escape from the circulating stream, unless the wall of the containing blood-vessel were ruptured. It is true that an English physiologist, Dr. Augustus Waller, affirmed in 1846, that he had seen blood-corpuscles, both red and white, pass bodily through the wall of the capillary vessel in which they were contained; and that, as no opening could be seen before their escape, so none could be observed afterwards—so rapidly was the part healed. But these observations did not attract much notice until the phenomena of escape of the blood-corpuscles from the capillaries and minute veins, apart from mechanical injury, was rediscovered by Professor Cohnheim in 1867.

Professor Cohnheim's experiment demonstrating the passage of the corpuscles through the wall of the blood-vessel, is performed in the following manner. A frog is curarized, that is to say, paralysis is produced by injecting under the skin a minute quantity of the poison called *curare*; and the abdomen having been opened, a portion of small intestine is drawn out, and its transparent mesentery spread out under a microscope. After a variable time, occupied by dilatation, following contraction, of the minute vessels, and accompanying quickening of the blood-stream, there ensues a retardation of the current; and blood-corpuscles, both red and white, begin to make their way through the capillaries and small veins. The process of extrusion of the white corpuscles is thus described by Dr. Burdon Sanderson, and the passage of the red corpuscles occurs after much the same fashion.

"Simultaneously with the retardation, the leucocytes, instead of loitering here and there at the edge of the axial current, begin to crowd in numbers against the vascular wall, as was long ago described by Dr. Williams. In this way the vein becomes lined with a continuous pavement of these bodies, which remain almost motionless, notwithstanding that the axial current sweeps by them as continuously as before, though with abated velocity. Now is the moment

at which the eye must be fixed on the outer contour of the vessel, from which (to quote Professor Cohnheim's words) here and there minute, colourless, button-shaped elevations spring, just as if they were produced by budding out of the wall of the vessel itself. The buds increase gradually and slowly in size, until each assumes the form of a hemispherical projection, of width corresponding to that of a leucocyte. Eventually the hemisphere is converted into a pear-shaped body, the small end of which is still attached to the surface of the vein, while the round part projects freely. Gradually the little mass of protoplasm removes itself further and further away, and, as it does so, begins to shoot out delicate prongs of transparent protoplasm from its surface, in nowise differing in their aspect from the slender thread by which it is still moored to the vessel. Finally the thread is severed, and the process is complete. The observer has before him an emigrant leucocyte, which in all appreciable respects resembles those which have been already described in the aqueous humour of the inflamed eye."

Various explanations of these remarkable phenomena have been suggested. Probably the nearest to the truth are those which attribute the chief share in the process to the vital endowments with respect to mobility and contractility of the parts concerned—both of the corpuscles (Bastian) and the capillary wall (Stricker). Dr. Sanderson remarks, "the capillary is not a dead conduit, but a tube of living protoplasm. There is no difficulty in understanding how the membrane may open to allow the escape of leucocytes, and close again after they have passed out; for it is one of the most striking peculiarities of contractile substance that when two parts of the same mass are separated, and again brought into contact, they melt together as if they had not been severed."

Hitherto, the escape of the corpuscles from the interior of the blood-vessels into the surrounding tissues has been studied chiefly in connection with pathology. But it is im-

possible to say, at present, to what degree the discovery may not influence all present notions regarding the nutrition of the tissues, even in health.

The circulation through the capillaries must, of necessity, be largely influenced by that which occurs in the vessels on either side of them—in the arteries or the veins; their intermediate position causing them to feel at once, so to speak, any alteration in the size or rate of the arterial or venous blood-stream. Thus, the apparent contraction of the capillaries, on the application of certain irritating substances, and during fear, and their dilatation in blushing, may be referred to the action of the small arteries, rather than to that of the capillaries themselves. But largely as the capillaries are influenced by these, and by the conditions of the parts which surround and support them, their own endowments must not be disregarded. They must be looked upon, not as mere passive canals for the passage of blood, but as possessing endowments of their own, in relation to the circulation. The capillary wall is, according to Stricker, actively living and contractile; and there is no reason to doubt that, as such, it must have an important influence in connection with that nutritive exchange which goes on without cessation between the blood within and the tissues outside the capillary vessel; a process which, under the name of vital capillary force, has long been recognised as one of the means concerned in the circulation of the blood.

The results of morbid action, as well as the phenomena of health, strongly support the notion of the existence of this so-called vital capillary attraction between the blood and the tissues. For example, when the access of oxygen to the lungs is prevented, the circulation through the pulmonic capillaries is gradually retarded, the blood-corpuscles cluster together, and their movement is eventually almost arrested, even while the action of the heart continues. In inflammation, also, the capillaries of

an inflamed part are enlarged and distended with blood, which either moves very slowly or is completely at rest. In both these cases the phenomena are local, and independent of the action of the heart, and appear to result from some alteration in the blood, which increases the adhesion of its particles to one another, and to the walls of the capillaries, to an amount which the propelling action of the heart is not able to overcome.

It may be concluded then, that the capillaries, which are formed of a simple cellular membrane, can of themselves exercise no such direct influence on the movement of their contents as to be at all comparable in degree to that which is exercised by the arteries or veins: yet that the constant interchange of relations between the blood within and the tissues outside these vessels does in some measure facilitate the movement of blood through the capillary system, and constitute one of the assistant forces of the circulation.

THE VEINS.

In *structure* the coats of veins bear a general resemblance to those of arteries. Thus, they possess an *outer*, *middle*, and *internal* coat. The *outer* coat is constructed of areolar tissue like that of the arteries, but is thicker. In some veins it contains muscular fibre-cells.

The *middle* coat is considerably thinner than that of the arteries; and, although it contains circular unstriped muscular fibres or fibre-cells, these are mingled with a larger proportion of yellow elastic and white fibrous tissue. In the large veins near the heart, namely, the *venæ cavæ* and pulmonary veins, the middle coat is replaced, for some distance from the heart, by circularly arranged striped muscular fibres, continuous with those of the auricles.

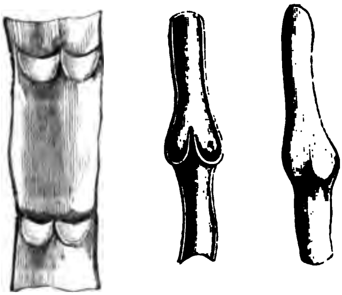
The *internal* coat of veins is less brittle than the corresponding coat of an artery, but in other respects resembles it closely.

The chief influence which the veins have in the circula-

tion, is effected with the help of the *valves*, which are placed in all veins subject to local pressure from the muscles between or near which they run. The general construction of these valves is similar to that of the semilunar valves of the aorta and pulmonary artery, already described (p. 108); but their free margins are turned in the opposite direction, *i.e. towards* the heart, so as to stop any movement of blood backward in the veins. They are commonly placed in pairs, at various distances in different veins, but almost uniformly in each (fig. 53). In the smaller veins, single valves are often met with; and three or four are sometimes placed together, or near one another, in the largest veins, such as the subclavian, and at their junction with the jugular veins.

Fig. 53.*

A B C



The valves are semilunar; the unattached edge being in some examples concave, in others straight. They are composed of inextensile fibrous tissue, and are covered with epithelium like that lining the veins. During the period of their inaction, when the venous blood is flowing in its proper direction, they lie by the sides of the veins; but when in action, they close together like the valves of the arteries, and offer a complete barrier to any backward movement of the blood (figs. 54 and 55).

Valves are not equally numerous in all veins, and in

Fig. 53. Diagrams showing valves of veins. A. Part of a vein laid open and spread out, with two pairs of valves. B. Longitudinal section of a vein, showing the apposition of the edges of the valves in their closed state. C. Portion of a distended vein, exhibiting a swelling in the situation of a pair of valves.

many they are absent altogether. They are most numerous in the veins of the extremities, and more so in those of the leg than the arm. They are commonly absent in veins of less than a line in diameter, and, as a general rule, there are few or none in those which are not subject to muscular pressure. Among those veins which have no valves may be mentioned the superior and inferior vena cava, the trunk and branches of the portal vein, the hepatic and renal veins, and the pulmonary veins; those in the interior of the cranium and vertebral column, those of the bones, and the trunk and branches of the umbilical vein are also destitute of valves.

The principal obstacle to the circulation is already overcome when the blood has traversed the capillaries; and the force of the heart which is not yet consumed, is sufficient to complete its passage through the veins, in which the obstructions to its movement are very slight. For the formidable obstacle supposed to be presented by the gravitation of the blood, has no real existence, since the pressure exercised by the column of blood in the arteries, will be always sufficient to support a column of venous blood of the same height as itself: the two columns mutually balancing each other. Indeed, so long as both arteries and veins contain continuous columns of blood, the force of gravitation, whatever be the position of the body, can have no power to move or resist the motion of any part of the blood in any direction. The lowest blood-vessels have, of course, to bear the greatest amount of pressure; the pressure on each part being directly proportionate to the height of the column of blood above it: hence their liability to distension. But this pressure bears equally on both arteries and veins, and cannot either move, or resist the motion of, the fluid they contain, so long as the columns of fluid are of equal height in both, and continuous. Their condition may, in this respect, be compared with that of a double bent tube, full of fluid, held vertically; whatever be the height and gravitation of

the columns of fluid, neither of them can move of its own weight, each being supported by the other; yet the least pressure on the top of either column will lift up the other: so, when the body is erect, the least pressure on the column of arterial blood may lift up the venous blood, and, were it not for the valves, the least pressure on the venous might lift up the arterial column.

In experiments to determine what proportion of the force of the left ventricle remains to propel the blood in the veins, Valentin found that the pressure of the blood in the jugular vein of a dog, as estimated by the hæmadynamometer, did not amount to more than $\frac{1}{11}$ or $\frac{1}{12}$ of that in the carotid artery of the same animal; and this estimate is confirmed, in the instances of several other arteries and their corresponding veins, by Mogk. In the upper part of the inferior vena cava, Valentin could scarcely detect the existence of any pressure, nearly the whole force received from the heart having been, apparently, consumed during the passage of the blood through the capillaries. But slight as this remaining force might be (and the experiment in which it was estimated would reduce the force of the heart below its natural standard), it would be enough to complete the circulation of the blood; for, as already stated, the spontaneous dilatation of the auricles and ventricles, though it may not be forcible enough to assist the movement of blood into them, is adapted to offer to that movement no obstacle.

Very effectual assistance to the flow of blood in the veins is afforded by the *action of the muscles* capable of pressing on such veins as have valves.

The *effect of muscular pressure* on such veins may be thus explained. When pressure is applied to any part of a vein, and the current of blood in it is obstructed, the portion behind the seat of pressure becomes swollen and distended as far back as to the next pair of valves. These, acting like the arterial valves, and being, like them, inextensile both in

themselves and at their margins of attachment, do not follow the vein in its distension, but are drawn out towards the axis of the canal. Then, if the pressure continues on the vein, the compressed blood, tending to move equally in all directions, presses the valves down into contact at their free edges, and they close the vein and prevent regurgitation of the blood. Thus, whatever force is exercised by the pressure of the muscles on the veins, is distributed partly in pressing the blood onwards in the proper course of the circulation, and partly in pressing it backwards and closing the valves behind.

The circulation might lose as much as it gains by such compression of the veins, if it were not for the numerous anastomoses by which they communicate, one with another;

*Fig. 54.**

Fig. 55.†

for through these, the closing up of the venous channel by the backward pressure is prevented from being any serious

* Fig. 54. Vein with valves open (Dalton).

† Fig. 55. Vein with valves closed; stream of blood passing off by lateral channel (Dalton).

hindrance to the circulation, since the blood, of which the onward course is arrested by the closed valves, can at once pass through some anastomosing channel, and proceed on its way by another vein (figs. 54 and 55). Thus, therefore, the effect of muscular pressure upon veins which have valves, is turned almost entirely to the advantage of the circulation; the pressure of the blood onwards is all advantageous, and the pressure of the blood backwards is prevented from being a hindrance by the closure of the valves and the anastomoses of the veins.

The effects of such muscular pressure are well shown by the acceleration of the stream of blood when, in venesection, the muscles of the fore-arm are put in action, and by the general acceleration of the circulation during active exercise; and the numerous movements which are continually taking place in the body while awake, though their single effects may be less striking, must be an important auxiliary to the venous circulation. Yet they are not essential; for the venous circulation continues unimpaired in parts at rest, in paralysed limbs, and in parts in which the veins are not subject to any muscular pressure.

Besides the assistance thus afforded by muscular pressure to the movement of blood along veins possessed of valves, it has been discovered by Mr. Wharton Jones that, in the web of the bat's wing, the veins are furnished with valves, and possess the remarkable property of rhythmical contraction and a dilatation, whereby the current of blood within them is distinctly accelerated. The contraction occurred, on an average, about ten times in a minute; the existence of valves preventing regurgitation, the entire effect of the contractions was auxiliary to the onward current of blood. Analogous phenomena have been now frequently observed in other animals.

Agents concerned in the Circulation of the Blood.

The agents concerned in the circulation of the blood which have been now described, may be thus enumerated :—

1. The action of the heart and of the arteries.

2. The vital capillary force exercised in the capillaries.

3. The possible slight action of the muscular coat of veins; and, much more, the contraction of muscles capable of acting on veins provided with valves.

It remains only to consider (4) the influence of the respiratory movements on the circulation.

Although the continuance of the respiratory movements is essential to the circulation of the blood, and although their cessation is followed, within a very few minutes, by that of the heart's action also, yet their direct mechanical influence on the movement of the current of blood is probably, under ordinary circumstances, but slight. The effect of expiration in increasing the pressure of the blood in the *arteries* is minutely illustrated by the experiments of Ludwig. It acts as the pressure of contracting muscles does upon the veins, and is advantageous to the onward movement of arterial blood, inasmuch as all movement backwards into the heart, which would otherwise occur at the same moment and from the same cause, is prevented by the force of the onward stream of blood from the contracting ventricle, and in the intervals of this contraction by the closure of the semilunar valves. Under ordinary circumstances, and with a free passage through the capillaries of the lungs, the effect of expiration on the stream of blood in the *veins* is also probably to assist, rather than retard its movement in the proper direction. For, with no obstruction in front, there is the force of the blood streaming into the heart from behind, to prevent any tendency to a backward flow, even

apart from what may be effected by the presence of the valves of the venous system.

It is true that in *violent* expiratory efforts there is a certain retardation of the circulation in the veins. The effect of such retardation is shown in the swelling-up of the veins of the head and neck, and the lividity of the face, during coughing, straining, and similar violent expiratory efforts; the effect shown in these instances being due both to some actual regurgitation of the blood in the great veins, and to the accumulation of blood in all the veins, from their being constantly more and more filled by the influx from the arteries.

But strong expiratory efforts, as in straining and the like, are not fairly comparable to ordinary expiration, inasmuch as they are instances of more or less interference with expiration, and involve probably circumstances leading to obstruction of the circulation in the pulmonary capillaries, such as are not present in the ordinary rhythmical exit of air from the lungs.

The act of *inspiration* is favourable to the venous circulation, and its effect is not counterbalanced by its tendency to draw the arterial, as well as the venous, blood towards the cavity of the chest. When the chest is enlarged in inspiration, the additional space within it is filled chiefly by the fresh quantity of air which passes through the trachea and bronchial passages to the vesicular structure of the lungs. But the blood being, like the air, subject to the atmospheric pressure, some of it also is at the same time pressed towards the expanding cavity of the chest, and therein towards the heart. The effect of this on the arterial current is hindered by the aortic valves, while they are closed, and by the forcible outward stream of blood from the ventricles when they are open; while, on the other hand, there is nothing to prevent an increased afflux of blood to the auricles through the large veins.

Sir David Barry was the first who showed plainly this

effect of inspiration on the venous circulation; and he mentions the following experiment in proof of it. He introduced one end of a bent glass tube into the jugular vein of an animal, the vein being tied above the point where the tube was inserted; the inferior end of the tube was immersed in some coloured fluid. He then observed that at the time of each inspiration the fluid ascended in the tube, while during expiration it either remained stationary, or even sank. Poiseuille confirmed the truth of this observation, in a more accurate manner, by means of his hæmadynamometer. And a like confirmation has been since furnished by Valentin, and in minute details by Ludwig.

The effect of inspiration on the veins is observable only in the large ones near the thorax. Poiseuille could not detect it by means of his instrument in veins more distant from the heart,—for example, in the veins of the extremities. And its beneficial effect would be neutralized were it not for the valves; for he found that, when he repeated Sir D. Barry's experiments, and passed the tube so far along the veins that it went beyond the valves nearest to the heart, as much fluid was forced back into the tube in every expiration as was drawn in through it in every inspiration.

Some secret experiments, by Dr. Burdon Sanderson, have proved more directly that inspiration is favourable to the circulation, inasmuch as, during it, the tension of the arterial system is increased. And it is only when the respiratory orifice is closed, as by plugging the trachea, that inspiratory efforts are sufficient to produce an opposite effect—to *diminish* the tension in the arteries.

On the whole, therefore, the respiratory movements of the chest are advantageous to the circulation.

Velocity of Blood in the Veins.

The *velocity* of the blood is greater in the veins than in the capillaries, but less than in the arteries: and with this

fact may be remembered the relative capacities of the arterial and venous systems; for since the veins return to the heart all the blood that they receive from it in a given time through the arteries, their larger size and proportionally greater number must compensate for the slower movement of the blood through them. If an accurate estimate of the proportionate areas of arteries and the veins corresponding to them could be made, we might, from the velocity of the arterial current, calculate that of the venous. An usual estimate is, that the capacity of the veins is about twice or three times as great as that of the arteries, and that the velocity of the blood's motion is, therefore, about twice or three times as great in the arteries as in the veins. Some doubt has, however, been lately expressed regarding the accuracy of this calculation, and the matter, therefore, must be considered not yet settled. The rate at which the blood moves in the veins gradually increases the nearer it approaches the heart, for the sectional area of the venous trunks, compared with that of the branches opening into them, becomes gradually less as the trunks advance towards the heart.

Velocity of the Circulation.

Having now considered the share which each of the circulatory organs has in the propulsion and direction of the blood, we may speak of their combined effects, especially in regard to the velocity with which the movement of the blood through the whole round of the circulation is accomplished. As Müller says, the rate of the blood's motion in the vessels must not be judged of by the rapidity with which it flows from a vessel when divided. In the latter case, the rate ot motion is the result of the entire pressure to which the whole mass of blood is subjected in the vascular system, and which at the point of the incision in the vessel meets with no resistance. In the closed vessels, on the contrary, no portion of blood can be moved forwards

except by impelling on the whole mass, and by overcoming the resistance arising from friction in the smaller vessels.

From the rate at which the blood escapes from opened vessels we can only judge, in general, that its velocity is, as already said, greater in arteries than in veins, and in both these greater than in the capillaries. More satisfactory data for the estimates are afforded by the results of experiments to ascertain the rapidity with which poisons introduced into the blood are transmitted from one part of the vascular system to another. From eighteen such experiments on horses, Hering deduced that the time required for the passage of a solution of ferrocyanide of potassium, mixed with the blood, from one jugular vein (through the right side of the heart, the pulmonary circulation, the left cavities of the heart, and the general circulation) to the jugular vein of the opposite side, varies from twenty to thirty seconds. The same substance was transmitted from the jugular vein to the great saphena in twenty seconds; from the jugular vein to the masseteric artery, in between fifteen and thirty seconds; to the facial artery, in one experiment, in between ten and fifteen seconds; in another experiment in between twenty and twenty-five seconds; in its transit from the jugular vein to the metatarsal artery, it occupied between twenty and thirty seconds, and in one instance more than forty seconds. The result was nearly the same whatever was the rate of the heart's action.

Poiseuille's observations accord completely with the above, and show, moreover, that when the ferrocyanide is injected into the blood with other substances, such as acetate of ammonia, or nitrate of potash (solutions of which, as other experiments have shown, pass quickly through capillary tubes), the passage from one jugular vein to the other is effected in from eighteen to twenty-four seconds; while, if instead of these, alcohol is added, the passage is not completed until from forty to forty-five seconds after injection. Still greater rapidity of transit

has been observed by Mr. J. Blake, who found that nitrate of baryta injected into the jugular vein of a horse could be detected in blood drawn from the carotid artery of the opposite side in from fifteen to twenty seconds after the injection. In sixteen seconds a solution of nitrate of potash, injected into the jugular vein of a horse, caused complete arrest of the heart's action, by entering and diffusing itself through the coronary arteries. In a dog, the poisonous effects of strychnia on the nervous system were manifested in twelve seconds after injection into the jugular vein; in a fowl, in six and a half seconds, and in a rabbit in four and a half seconds.

In all these experiments, it is assumed that the substance injected moves with the blood, and at the same rate as it, and does not move from one part of the organs of circulation to another by diffusing itself through the blood or tissues more quickly than the blood moves. The assumption is sufficiently probable, to be considered nearly certain, that the times above-mentioned, as occupied in the passage of the injected substances, are those in which the portion of blood, into which each was injected, was carried from one part to another of the vascular system. It would, therefore, appear that a portion of blood can traverse the entire course of the circulation, in the horse, in half a minute; of course it would require longer to traverse the vessels of the most distant part of the extremities than to go through those of the neck; but taking an average length of vessels to be traversed, and assuming, as we may, that the movement of blood in the human subject is not slower than in the horse, it may be concluded that one minute, which is the estimate usually adopted of the average time in which the blood completes its entire circuit in man, is rather above than below the actual rate.

Another mode of estimating the general velocity of the circulating blood, is by calculating it from the quantity of blood supposed to be contained in the body, and from the

quantity which can pass through the heart in each of its actions. But the conclusions arrived at by this method are less satisfactory. For the estimates both of the total quantity of blood, and of the capacity of the cavities of the heart, have as yet only approximated to the truth. Still, the most careful of the estimates thus made accord with those already mentioned; for Valentin has, from these data, calculated that the blood may all pass through the heart in from $43\frac{3}{4}$ to $62\frac{2}{3}$ seconds.

The estimate for the speed at which the blood may be seen moving in transparent parts, is not opposed to this. For, as already stated (p. 162), though the movement through the capillaries may be very slow, yet the length of capillary vessel through which any portion of blood has to pass is very small. Even if we estimate that length at the tenth of an inch, and suppose the velocity of the blood therein to be only one inch per minute, then each portion of blood may traverse its own distance of the capillary system in about six seconds. There would thus be plenty of time left for the blood to travel through its circuit in the larger vessels, in which the greatest length of tube that it can have to traverse in the human subject does not exceed ten feet.

All the estimates here given are averages; but of course the time in which a given portion of blood passes from one side of the heart to the other, varies much according to the organ it has to traverse. The blood which circulates from the left ventricle, through the coronary vessels, to the right side of the heart, requires a far shorter time for the completion of its course than the blood which flows from the left side of the heart to the feet, and back again to the right side of the heart; for the circulation from the left to the right cavities of the heart may be represented as forming a number of arches, varying in size, and requiring proportionately various times for the blood to traverse them; the smallest of these arches being formed by the

circulation through the coronary vessels of the heart itself. The course of the blood from the right side of the heart, through the lungs to the left, is shorter than most of the arches described by the systemic circulation, and in it the blood flows, *cæteris paribus*, much quicker than in most of the vessels which belong to the aortic circulation. For although the quantity of blood contained, at any instant, in the greater circulation of the body, is far greater than the quantity within the lesser circulation; yet, in any given space of time, as much blood must pass through the lungs as passes in the same time through the systemic circulation. If the systemic vessels contain five times as much blood as the pulmonary, the blood in them must move five times as slow as in these; else, the right side of the heart would be either overfilled or not filled enough.

Peculiarities of the Circulation in different Parts.

The most remarkable peculiarities attending the circulation of blood through different organs are observed in the cases of the *lungs*, the *liver*, the *brain*, and the *erectile organs*. The pulmonary and portal circulations have been already alluded to (pp. 101, 102), and will be again noticed when considering the functions of the lungs and liver.

The chief circumstances requiring notice, in relation to the *cerebral circulation*, are observed in the arrangement and distribution of the vessels of the brain, and in the conditions attending the amount of blood usually contained within the cranium.

The functions of the brain seem to require that it should receive a large supply of blood. This is accomplished through the number and size of its arteries, the two internal carotids, and the two vertebrals. But it appears to be further necessary that the force with which this blood is sent to the brain should be less, or at least, subject to less variation from external circumstances than it is in other parts. This object is effected by several provisions; such

as the tortuosity of the large arteries, and their wide anastomoses in the formation of the circle of Willis, which will insure that the supply of blood to the brain may be uniform, though it may by an accident be diminished, or in some way changed, through one or more of the principal arteries. The transit of the large arteries through bone, especially the carotid canal of the temporal bone, may prevent any undue distension; and uniformity of supply is further insured by the arrangement of the vessels in the pia mater, in which, previous to their distribution to the substance of the brain, the large arteries break up and divide into innumerable minute branches ending in capillaries, which, after frequent communications with one another, enter the brain, and carry into nearly every part of it uniform and equable streams of blood.

The arrangement of the *veins* within the cranium is also peculiar. The large venous trunks or sinuses are formed so as to be scarcely capable of change of size; and composed, as they are, of the tough tissue of the dura mater, and, in some instances, bounded on one side by the bony cranium, they are not compressible by any force which the fulness of the arteries might exercise through the substance of the brain; nor do they admit of distension when the flow of venous blood from the brain is obstructed.

The general uniformity in the supply of blood to the brain, which is thus secured, is well adapted, not only to its functions, but also to its condition as a mass of nearly incompressible substance placed in a cavity with unyielding walls. These conditions of the brain and skull have appeared, indeed, to some, enough to justify the opinion that the quantity of blood in the brain must be at all times the same; and that the quantity of blood received within any given time through the arteries must be always, and at the same time, exactly equal to that removed by the veins. In accordance with this supposition, the symptoms commonly referred to either excess or deficiency of blood

in the brain, were ascribed to a disturbance in the balance between the quantity of arterial and that of venous blood. Some experiments performed by Dr. Kellie appeared to establish the correctness of this view. But Dr. Burrows having repeated these experiments, and performed additional ones, obtained different results. He found that in animals bled to death, without any aperture being made in the cranium, the brain became pale and anæmic like other parts. And in proof that, during life, the cerebral circulation is influenced by the same general circumstances that influence the circulation elsewhere, he found congestion of the cerebral vessels in rabbits killed by strangling or drowning; while in others, killed by prussic acid, he observed that the quantity of blood in the cavity of the cranium was determined by the position in which the animal was placed after death, the cerebral vessels being congested when the animal was suspended with its head downwards, and comparatively empty when the animal was kept suspended by the ears. He concluded, therefore, that although the total volume of the contents of the cranium is probably nearly always the same, yet the quantity of blood in it is liable to variation, its increase or diminution being accompanied by a simultaneous diminution or increase in the quantity of the cerebro-spinal fluid, which, by readily admitting of being removed from one part of the brain and spinal cord to another, and of being rapidly absorbed, and as readily effused, would serve as a kind of supplemental fluid to the other contents of the cranium, to keep it uniformly filled in case of variations in their quantity. And there can be no doubt that, although the arrangements of the blood-vessels, to which reference has been made, ensure to the brain an amount of blood which is tolerably uniform, yet, inasmuch as with every beat of the heart and every act of respiration, and under many other circumstances, the quantity of blood in the cavity of the cranium is constantly varying, it is plain that,

were there not provision made for the possible displacement of some of the contents of the unyielding bony case in which the brain is contained, there would be often alternations of excessive pressure with insufficient supply of blood. Hence we may consider that the cerebro-spinal fluid in the interior of the skull not only subserves the mechanical functions of fat in other parts as a *packing* material, but by the readiness with which it can be displaced into the spinal canal, provides the means whereby undue pressure and insufficient supply of blood are equally prevented.

Circulation in erectile structures.—The instances of greatest variation in the quantity of blood contained, at different times, in the same organs, are found in certain structures which, under ordinary circumstances, are soft and flaccid, but, at certain times, receive an unusually large quantity of blood, become distended and swollen by it, and pass into the state which has been termed *erection.* Such structures are the corpora cavernosa and corpus spongiosum of the penis in the male, and the clitoris in the female; and, to a less degree, the nipple of the mammary gland in both sexes. The corpus cavernosum penis, which is the best example of an erectile structure, has an external fibrous membrane or sheath; and from the inner surface of the latter are prolonged numerous fine lamellæ which divide its cavity into small compartments looking like cells when they are inflated. Within these is situated the plexus of veins upon which the peculiar erectile property of the organ mainly depends. It consists of short veins which very closely interlace and anastomose with each other in all directions, and admit of great variation of size, collapsing in the passive state of the organ, but, for erection, capable of an amount of dilatation which exceeds beyond comparison that of the arteries and veins which convey the blood to and from them. The strong fibrous tissue lying in the intervals of the venous plexuses, and the external

fibrous membrane or sheath with which it is connected, limit the distension of the vessels, and, during the state of erection, give to the penis its condition of tension and firmness. The same general condition of vessels exists in the corpus spongiosum urethræ, but around the urethra the fibrous tissue is much weaker than around the body of the penis, and around the glans there is none. The venous blood is returned from the plexuses by comparatively small veins; those from the glans and the fore part of the urethra empty themselves into the dorsal vein of the penis; those from the corpus cavernosum pass into deeper veins which issue from the corpora cavernosa at the crura penis; and those from the rest of the urethra and bulb pass more directly into the plexus of the veins about the prostate. For all these veins one condition is the same; namely, that they are liable to the pressure of muscles when they leave the penis. The muscles chiefly concerned in this action are the erector penis and accelerator urinæ.

Erection results from the distension of the venous plexuses with blood. The principal exciting cause in the erection of the penis is nervous irritation, originating in the part itself, or derived from the brain and spinal cord. The nervous influence is communicated to the penis by the pudic nerves, which ramify in its vascular tissue: and Guenther has observed, that, after their division in the horse, the penis is no longer capable of erection. It affords a good example of the subjection of the circulation in an individual organ to the influence of the nerves; but the mode in which they excite a greater influx of blood is not with certainty known.

The most probable explanation is that offered by Professor Kölliker, who ascribes the distension of the venous plexuses to the influence of organic muscular fibres, which are found in abundance in the corpora cavernosa of the penis, from the bulb to the glans, also in the clitoris and

other parts capable of erection. While erectile organs are flaccid and at rest, these contractile fibres exercise an amount of pressure on the plexuses of vessels distributed amongst them, sufficient to prevent their distension with blood. But when through the influence of their nerves, these parts are stimulated to erection, the action of these fibres is suspended, and the plexuses thus liberated from pressure, yield to the distending force of the blood, which, probably, at the same time arrives in greater quantity, owing to a simultaneous dilatation of the arteries of the parts, and thus the plexuses become filled, and remain so until the stimulus to erection subsides, when the organic muscular fibres again contract, and so gradually expel the excess of blood from the previously distended vessels. The influence of cold in producing extreme contraction and shrinking of erectile organs, and the opposite effect of warmth in inducing fulness and distension of these parts, are among the arguments used by Kölliker in support of this opinion.

The accurate dissections and experiments of Kobelt, extending and confirming those of Le Gros Clark and Krause, have shown, that this influx of the blood, however explained, is the first condition necessary for erection, and that through it alone much enlargement and turgescence of the penis may ensue. But the erection is probably not complete, nor maintained for any time except when, together with this influx, the muscles already mentioned contract, and by compressing the veins, stop the efflux of blood, or prevent it from being as great as the influx.

It appears to be only the most perfect kind of erection that needs the help of muscles to compress the veins; and none such can materially assist the erection of the nipples, or that amount of turgescence, just falling short of erection, of which the spleen and many other parts are capable. For such turgescence nothing more seems necessary than a large plexiform arrangement of the veins, and such

arteries as may admit, upon local occasions, augmented quantities of blood.

The Influence of the Nervous System on the circulation in the blood-vessels will be considered in Chap. XVII.

CHAPTER VII.

RESPIRATION.

As the blood circulates through the various parts of the body, and fulfils its office by nourishing the several tissues, by supplying to secreting organs the materials necessary for their secretions, and by the performance of other duties with which it is charged, it is deprived of part of its nutritive constituents, and receives impurities which need removal from the body. It is, therefore, necessary that fresh supplies of nutriment should be continually added to the blood, and that provision should be made for the removal of the impurities. The first of these objects is accomplished by the processes of digestion and absorption. The second is principally effected by the agency of the various excretory organs, through which are removed the several impurities with which the blood is charged, whether these impurities are derived altogether from the degenerations of tissue, or in part also from the elements of unassimilated food. One of the most important and abundant of the impurities is carbonic acid, the removal of which and the introduction of fresh quantities of oxygen, constitute the chief purpose of respiration—a

process which, because of its intimate relation to the circulation, may be considered here, rather than with the other excretory functions.

Position and Structure of the Lungs.

The lungs occupy the greater portion of the chest, or uppermost of the two cavities into which the body is divided by the diaphragm (fig. 31). They are of a spongy elastic texture, and on section appear to the naked eye as if they were in great part solid organs, except here and there, at certain points, where branches of the bronchi or air-tubes may have been cut across, and show, on their surface of the section, their tubular structure.

In fact, however, the lungs are hollow organs, and we may consider them as really two bags containing air, each of which communicates by a separate orifice with a common air-tube (fig. 31), through the upper portion of which, the *larynx*, they freely communicate with the external

Fig. 56.*

atmosphere. The orifice of the larynx is guarded by muscles, and can be opened or closed at will.

* Fig. 56. Transverse section of the chest (after Gray).

It has been said, in the preceding chapter that each lung is enveloped in a distinct fibrous bag, with a smooth, slippery lining, and that the outer smooth surface of the lung glides easily on the inner smooth surface of the bag which envelops it. This enveloping bag, which is called the pleura, is easily seen in the dead subject; and when it is opened, as in an ordinary *post-mortem* examination, there is a considerable space left, by the elastic recoil of the lung, between the outer surface of the lung and the inner surface of the pleura, which is left sticking, so to speak, to the inner suface of the walls and floor of the chest.

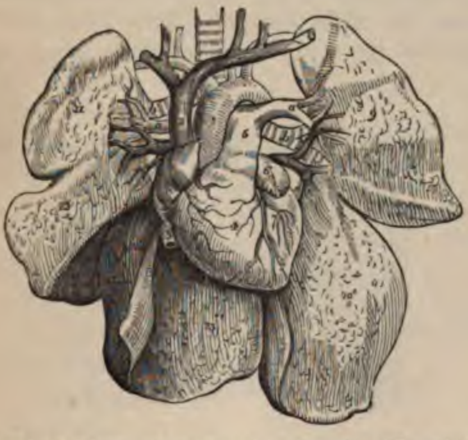
This space, however, between the lung and the pleura does not exist (except in some cases of disease) so long as the chest is not opened; and, while considering the subject of normal healthy respiration, we may discard altogether the notion of any space or cavity between the lung and the wall of the chest. So far as the movement of the lung is concerned it might be adherent completely to the chest-wall, inasmuch as they accompany each other in all their movements; only there is a slight gliding of the smooth surface of the lung on the smooth inner surface of the pleura, but no separation, in the slightest degree, of one from the other.*

The *trachea*, or tube through which air passes to the lungs, divides into two branches—one for each lung; and these primary branches, or *bronchi*, after entering the

* It may be mentioned, that the smooth covering of the lung is really continuous with the inner smooth lining of the walls and floor of the chest, as will be readily seen in fig. 56. Hence the membrane which covers the lung is called the *visceral* layer of the pleura, and that which lines the walls and floor of the chest the *parietal* layer. The appearance of a cavity or space (fig. 56) between the visceral layer of pleura (covering the lungs) and the parietal layer (covering the inner surface of the wall of the chest and upper part of the diaphragm) is only inserted for the sake of distinctness.

substance of the organ, divide and subdivide into a number of smaller and smaller branches, which penetrate to every part of the organ, until at length they end in the smaller subdivisions of the lung called *lobules*. All the larger branches have walls formed of tough membrane, containing portions of cartilaginous rings, by which they are held open, and unstriped muscular fibres, as well as longitudinal bundles of elastic tissue. They are lined by mucous membrane, the surface of which, like that of the

Fig. 57.*



larynx and trachea, is covered with vibratile ciliary epithelium (fig. 58).

As the bronchi divide they become smaller and smaller,

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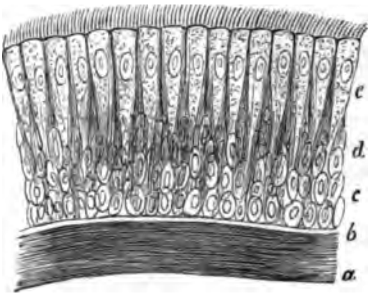
* Fig. 57. A diagrammatic representation of the heart and great vessels in connection with the lungs—$\frac{1}{8}$. The pericardium has been removed, and the lungs are turned aside. 1, right auricle; 2, vena cava superior; 3, vena cava inferior; 4, right ventricle; 5, stem of the pulmonary artery; *a a*, its right and left branches; 6, left auricular appendage; 7, left ventricle; 8, aorta; 9, 10, the two lobes of the left lung; 11, 12, 13, the three lobes of the right lung; *b b*, right and left bronchi; *v v*, right and left upper pulmonary veins.

and their walls thinner; the cartilaginous rings, especially becoming scarcer and more irregular, until, in the smaller bronchial tubes, they are represented only by minute and scattered cartilaginous flakes. And when the bronchi, by successive branches, are reduced to about $\frac{1}{40}$ of an inch in diameter, they lose their cartilaginous element altogether, and their walls are formed only of a tough, fibrous, elastic membrane, with traces of circular muscular fibres; they are still lined, however, by a thin mucous membrane, with ciliated epithelium.

Each lung is partially subdivided into separate portions, called *lobes;* the right lung into three lobes, and the left lung into two (fig. 57). Each of these lobes, again, is

Fig. 58.*



composed of a large number of minute parts, called *lobules.* Each pulmonary lobule may be considered a lung in miniature, consisting, as it does, of a branch of the bronchial tube, of air-cells, blood-vessels, nerves, and lymphatics, with a sparing amount of areolar tissue.

On entering a lobule, the small bronchial tube divides

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* Fig. 58. Ciliary epithelium of the human trachea magnified 350 diameters. *a*, Layer of longitudinally arranged elastic fibres; *b*, Basement membrane; *c*, Deepest cells, circular in form; *d*, Intermediate elongated cells; *e*, Outermost layer of cells fully developed and bearing cilia (after Kölliker).

[redacted]

and subdivides; its walls, at the same time, becoming thinner and thinner, until at length they are formed only of a thin membrane of areolar and elastic tissue, lined by a layer of *squamous* epithelium, not provided with cilia. At the same time, they are altered in shape; each of the minute terminal branches widening out funnel-wise, and its walls being pouched out irregularly into small saccular dilatations, called air-cells (fig. 59). Such a funnel-shaped terminal branch of the bronchial tube, with its group of pouches or air-cells, has been called an *infundibulum* (fig. 59), and the irregular oblong space in its centre, with which the air-cells communicate, an *intercellular passage.*

Fig. 59.*

The air-cells may be placed singly, like recesses from the intercellular passage, but more often they are arranged in groups or even in rows, like minute sacculated tubes; so that a short series of cells, all communicating with one another, open by a common orifice into the tube. The cells are of various forms, according to the mutual pressure to which they are subject; their walls are nearly in contact, and they vary from $\frac{1}{50}$ to $\frac{1}{70}$ of an inch in diameter. Their walls are formed of fine membrane, similar to that of the intercellular passages, and continuous with it, which membrane is

* Fig. 59. Two small groups of air-cells, or *infundibula, a a,* with air-cells, *b b,* and the ultimate bronchial tubes, *c c,* with which the air-cells communicate. From a new-born child (after Kölliker).

folded on itself so as to form a sharp-edged border at each circular orifice of communication between contiguous air-cells, or between the cells and the bronchial passages. Numerous fibres of elastic tissue are spread out between contiguous air-cells, and many of these are attached to the outer surface of the fine membrane of which each cell is composed, imparting to it additional strength, and the power of recoil after distension (fig. 60, *b* and *c*). The

Fig. 60.*

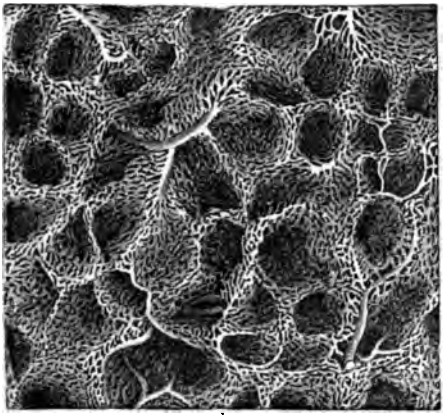
cells are lined by a layer of *squamous* or *tessellated* epithelium, not provided with cilia. Outside the cells, a network of pulmonary capillaries is spread out so densely (fig. 61), that the interspaces or meshes are even narrower

* Fig. 60. Air-cells of lung, magnified 350 diameters. *a*, Epithelial lining of the cells; *b*, Fibres of elastic tissue; *c*, Delicate membrane of which the cell-wall is constructed with elastic fibres attached to it (after Kölliker).

than the vessels, which are, on an average, $\frac{1}{3000}$ of an inch in diameter. Between the atmospheric air in the cells and the blood in these vessels, nothing intervenes but the thin membranes of the cells and capillaries and the delicate epithelial lining of the former; and the exposure of the blood to the air is the more complete, because the folds of membrane between contiguous cells, and often the spaces between the walls of the same, contain only a single layer of capillaries, both sides of which are thus at once exposed to the air.

The cells situated nearest to the centre of the lung are smaller, and their networks of capillaries are closer than those nearer to the circumference, in adaptation to the

Fig. 61.*



more ready supply of fresh air to the central than the peripheral portion of the lungs. The cells of adjacent lobules do not communicate; and those of the same lobule, or proceeding from the same intercellular passage, do so as a general rule only near angles of bifurcation; so that,

* Fig. 61. Capillary net-work of the pulmonary blood-vessels in the human lung (from Kölliker) $\frac{60}{1}$.

when any bronchial tube is closed or obstructed, the supply of air is lost for all the cells opening into it or its branches.

Mechanism of Respiration.

For the proper understanding of the mechanism by which air enters and is expelled from the lungs, the following facts must be borne in mind:—

The lungs form two distinct hollow bags (communicating with the exterior through the trachea and larynx), and are always closely in contact with the inner surface of the chest walls, while their lower portions are closely in contact with the diaphragm, or muscular partition which separates the chest from the abdomen (figs. 31 and 65). The lungs follow all movements of the parts in contact with them; and for the evident reason that the outer surface of the lung-bag not being exposed directly to atmospheric pressure, while the inner surface is so exposed, the pressure from within preserves the lungs in close contact with the parts surrounding them, and obliterates, practically, the pleural space, and must continue to do so, until from some cause or other—say from an opening for the admission of air through the chest-walls, the pressure on the outside of the lung equals or exceeds that on the interior. Any such artificial condition of things, however, need not here be considered.

For the inspiration of air into the lungs it will be evident from the foregoing facts, that all that is necessary is such a movement of the side-walls or floor of the chest, or of both, that the capacity of the interior shall be enlarged. By such increase of capacity there will be of course a diminution of the pressure of the air in the lungs, and a fresh quantity will enter through the larynx and trachea to equalise the pressure on the inside and outside of the chest. For the expiration of air, on the other hand, *it is also* evident, that, by an opposite movement which

shall contract the capacity of the chest, the pressure in the interior will be increased, and air will be expelled, until the pressures within and without the chest are again equal. In both cases the air passes through the trachea and larynx, whether in entering or leaving the lungs, there being no other communication with the exterior, and the lung, for the reason before mentioned, remains under all the circumstances described, closely in contact with the walls and floor of the chest. To speak of expansion of the chest, is to speak also of expansion of the lung.

We have now to consider the means by which the chest-cavity is alternately enlarged and contracted for the entrance and expulsion of atmospheric air; or, in technical terms, for *inspiration* and *expiration*.

Respiratory Movements.

The chest is a cavity filled by the lungs, heart, and large blood-vessels, etc., and closed everywhere against the entrance of air except by the way of the larynx and trachea. It is bounded behind and at the sides by the spine and ribs, and in front by the sternum and cartilages of the ribs. Its floor is formed mainly by the diaphragm.

The immediate inner lining of all these parts is the outer or polished layer of the pleura; and this membrane also is stretched continuously across the top of the chest-cavity, and mainly forms its roof.

The enlargement of the capacity of the chest in *inspiration* is a muscular act; the muscles concerned in producing the effect being chiefly the diaphragm and the *external* intercostal muscles, with that part of the *internal* intercostal which is between the cartilages of the ribs. These are assisted by the levatores costarum, the serratus posticus superior, and some others.

The *vertical* diameter of the chest is increased by the contraction and consequent descent of the diaphragm,—the sides of the muscle descending most, and the central

tendon remaining comparatively unmoved while the intercostal, and other muscles just mentioned, by acting at the same time, not only prevent the diaphragm during its contraction from drawing in the sides of the chest, but increase the diameter of the chest in the *lateral* direction, by elevating the ribs; that is to say, by rotating them, to speak roughly, around an axis passing through their sternal and spinal attachments,—somewhat after the fashion of raising the handle of a bucket (fig. 62). This is not all, however. Another effect of the contraction of the intercostal muscles is to increase the *antero-posterior*

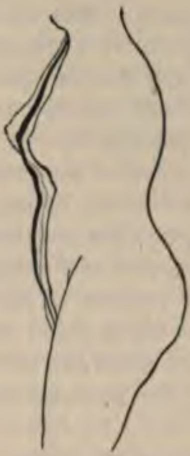
Fig. 62.

diameter of the chest,—by partially straightening out the angle between the rib and its cartilage, and thus lengthening the distance between its spinal and sternal attachments (fig. 62, A). In this way, at the same time that the ribs are raised, the sternum is pushed forward. This forward movement of the sternum, which is accompanied by a slight upward movement, is in part accomplished also by a raising of the anterior extremities of the rib cartilages, which of course, in any movement, carry the sternum with them. The differences in shape and direction of the upper and lower true ribs, and the more acute angles formed by

the junction of the latter with their cartilages, make the effect much greater at the lower than at the upper part of the chest.

Fig. 63.*

Fig. 64.†



The expansion of the chest in inspiration presents some

* Fig. 63 (after Hutchinson). The changes of the thoracic and abdominal walls of the male during respiration. The back is supposed to be fixed in order to throw forward the respiratory movement as much as possible. The outer black continuous line in front represents the ordinary breathing movement: the anterior margin of it being the boundary of inspiration, the posterior margin the limit of expiration. The line is thicker over the abdomen, since the ordinary respiratory movement is chiefly abdominal: thin over the chest, for there is less movement over that region. The dotted line indicates the movement on deep inspiration, during which the sternum advances while the abdomen recedes.

† Fig. 64 (after Hutchinson). The respiratory movement in the female. The lines indicate the same changes as in the last figure. The thickness of the continuous line over the sternum shows the larger extent of the ordinary breathing movement over that region in the female than in the male.

peculiarities in different persons and circumstances. In young children, it is effected almost entirely by the diaphragm, which being highly arched in expiration, becomes flatter as it contracts, and, descending, presses on the abdominal viscera, and pushes forward the front walls of the abdomen. The movement of the abdominal walls being here more manifest than that of any other part, it is usual to call this the *abdominal mode* or *type* of respiration. In adult men, together with the descent of the diaphragm, and the pushing forward of the front wall of the abdomen, the lower part of the chest and the sternum are subject to a wide movement in inspiration. In women, the movement appears less extensive in the lower, and more so in the upper, part of the chest; a mode of breathing to which a greater mobility of the first rib is adapted, and which may have for its object the provision of sufficient space for respiration when the lower part of the chest is encroached upon by the pregnant uterus. MM. Beau and Maissiat call the former the *inferior costal*, and the latter the *superior costal*, type of respiration; but the annexed diagrams will explain the difference better than the names will, for these imply a greater diversity than naturally exists in the modes of inspiration.

From the enlargement produced in inspiration, the chest and lungs return in ordinary tranquil expiration, by their elasticity; the force employed by the inspiratory muscles in distending the chest and overcoming the elastic resistance of the lungs and chest-walls, being returned as an expiratory effort when the muscles are relaxed. This elastic recoil of the rib-cartilages, but also of the lungs themselves, in consequence of the elastic tissue which they contain in considerable quantity, is sufficient, in ordinary quiet breathing, to expel air from the chest in the intervals of inspiration, and no muscular power is required. In all voluntary expiratory efforts, however, as in speaking, singing, blowing, and the like, and in many involuntary

actions also, as sneezing, coughing, etc., something more than merely passive elastic power is of course necessary, and the proper expiratory muscles are brought into action. By far the chief of these are the abdominal muscles, which, by pressing on the viscera of the abdomen, push up the floor of the chest formed by the diaphragm, and by thus making pressure on the lungs, expel air from them through the trachea and larynx. All muscles, however, which depress the ribs, must act also as muscles of expiration, and therefore we must conclude that the abdominal muscles are assisted in their action by the greater part of the internal intercostals, the triangularis sterni, the serratus posticus inferior, etc. When by the efforts of the expiratory muscles, the chest has been squeezed to less than its average diameter, it again, on relaxation of the muscles, returns to the normal dimensions by virtue of its elasticity. The construction of the chest-walls, therefore, admirably adapts them for recoiling against and resisting as well undue contraction as undue dilatation.

As before mentioned, the lungs, after distension in the act of inspiration, contract by virtue of the elastic tissue which is present in the bronchial tubes, on and between the air-cells, and in the investing pleura. But in the natural condition of the parts, they can never contract to the utmost, but are always more or less "on the stretch," being kept closely in contact with the inner surface of the walls of the chest by atmospheric pressure, able to act only on their interior, and can contract away from these only when, by some means or other, as by making an opening into the pleural cavity, or by the effusion of fluid there, the pressure on the exterior and interior of the lungs becomes equal. Thus, under ordinary circumstances, the degree of contraction or dilatation of the lungs is dependent on that of the boundary walls of the chest, the outer surface of the one being in close contact with the inner surface of the other, and obliged to follow it in all its movements.

Respiratory Rhythm.

The acts of expansion and contraction of the chest, take up under ordinary circumstances a nearly equal time, and can scarcely be said to be separated from each other by an intervening pause.

The act of inspiring air, however, especially in women and children, is a little shorter than that of expelling it, and there is commonly a very slight pause between the end of expiration and the beginning of the next inspiration. The respiratory rhythm may be thus expressed :—

Inspiration	6
Expiration	7 or 8

A very slight pause.

Respiratory Movements of the Glottis.

During the action of the muscles which directly draw air into the chest, those which guard the opening through which it enters are not passive. In hurried breathing the instinctive dilatation of the nostrils is well seen, although under ordinary conditions it may not be noticeable. The opening at the upper part of the larynx, however, or rima glottidis (fig. 65), is dilated at each inspiration, for the more ready passage of air, and collapses somewhat at each expiration, its condition, therefore, corresponding during respiration with that of the walls of the chest. There is a further likeness between the two acts in that, under ordinary circumstances, the dilatation of the rima glottidis is a muscular act, and its contraction chiefly an elastic recoil; although, under various conditions, to be hereafter mentioned, there may be, in the contraction of the glottis, considerable muscular power exercised.

Quantity of Air Respired.

The quantity of air that is changed in the lungs in each act of ordinary tranquil breathing is variable, and is very difficult to estimate, because it is hardly possible to breathe naturally while, as in an experiment, one is attending to the process. Probably 30 to 35 cubic inches are a fair average in the case of healthy young and middle-aged men; but Bourgery is perhaps right in saying, that old people, even in health, habitually breathe more deeply, and change in each respiration a larger quantity of air than younger persons do.

The total quantity of air which passes into and out of the lungs of an adult, at rest, in 24 hours, has been estimated by Dr. E. Smith at about 686,000 cubic inches. This quantity, however, is largely increased by exertion; and the same observer has computed the average amount for a hard-working labourer in the same time, at 1,568,390 cubic inches.

The quantity which is habitually and almost uniformly changed in each act of breathing, is called by Mr. Hutchinson *breathing air.* The quantity over and above this which a man can draw into the lungs in the deepest inspiration, he names *complemental air:* its amount is various, as will be presently shown. After ordinary expiration, such as that which expels the *breathing air*, a certain quantity of air remains in the lungs, which may be expelled by a forcible and deeper expiration: this he terms *reserve air.* But, even after the most violent expiratory effort, the lungs are not completely emptied; a certain quantity always remains in them, over which there is no voluntary control, and which may be called *residual air.* Its amount depends in great measure on the absolute size of the chest, and has been variously estimated at from forty to two hundred and sixty cubic inches.

The greatest respiratory capacity of the chest is indi-

cated by the quantity of air which a person can expel from his lungs by a forcible expiration after the deepest inspiration that he can make. Mr. Hutchinson names this the *vital capacity:* it expresses the power which a person has of breathing in the emergencies of active exercise, violence, and disease; and in healthy men it varies according to *stature*, *weight*, and *age*.

It is found by Mr. Hutchinson, from whom most of our information on this subject is derived, that at a temperature of 60° F., 225 cubic inches is the average *vital capacity* of a healthy person, five feet seven inches in height. For every inch of height above this standard the capacity is increased, on an average, by eight cubic inches; and for every inch below, it is diminished by the same amount. This relation of capacity to height is quite independent of the absolute capacity of the cavity of the chest; for the cubic contents of the chest do not always, or even generally, increase with the stature of the body; and a person of small absolute capacity of chest may have a large capacity of respiration, and *vice versâ.* The capacity of respiration is determined only by the mobility of the walls of the chest; but why this mobility should increase in a definite ratio with the height of the body is yet unexplained, and must be difficult of solution, seeing that the height of the body is chiefly determined by that of the legs, and not by the height of the trunk or the depth of the chest. But the vast number of observations made by Mr. Hutchinson seem to leave no doubt of the fact as stated above.

The influence of *weight* on the capacity of respiration is less manifest and considerable than that of height: and it is difficult to arrive at any definite conclusions on this point, because the natural average weight of a healthy man in relation to stature has not yet been determined. As a general statement, however, it may be said that the capacity of respiration is not affected by weights under 161 pounds, or 11½ stones; but that, above this point, it

is diminished at the rate of one cubic inch for every additional pound up to 196 pounds, or 14 stones; so that, for example, while a man of five feet six inches, and weighing less than 11½ stones, should be able to expire 217 cubic inches, one of the same height, weighing 12½ stones, might expire only 203 cubic inches.

By *age*, the capacity appears to be increased from about the fifteenth to the thirty-fifth year, at the rate of five cubic inches per year, from thirty-five to sixty-five it diminishes at the rate of about one and a-half cubic inch per year; so that the capacity of respiration of a man of sixty years old would be about 30 cubic inches less than that of a man forty years old, of the same height and weight.

Mr. Hutchinson's observations were made almost exclusively on men; and his conclusions are, perhaps, true of them alone; for women, according to Bourgery, have only half the capacity of breathing that men of the same age have.

The *number* of respirations in a healthy adult person usually ranges from fourteen to eighteen per minute.

It is greater in infancy and childhood; and of course varies much according to different circumstances, such as exercise or rest, health or disease, etc. Variations in the number of respirations correspond ordinarily with similar variations in the pulsations of the heart. In health the proportion is about 1 to 4, or 1 to 5, and when the rapidity of the heart's action is increased, that of the chest movement is commonly increased also; but not in every case in equal proportion. It happens occasionally in disease, especially of the lungs or air-passages, that the number of respiratory acts increases in quicker proportion than the beats of the pulse; and, in other affections, much more commonly, that the number of the pulses is greater in proportion than that of the respirations.

According to Mr. Hutchinson, the *force* with which the

inspiratory muscles are capable of acting, is greatest in individuals of the height of from five feet seven inches to five feet eight inches, and will elevate a column of three inches of mercury. Above this height, the force decreases as the stature increases; so that the average of men of six feet can elevate only about two and a half inches of mercury. The force manifested in the strongest expiratory acts is, on the average, one-third greater than that exercised in inspiration. But this difference is in great measure due to the power exerted by the elastic reaction of the walls of the chest; and it is also much influenced by the disproportionate strength which the expiratory muscles attain, from their being called into use for other purposes than that of simple expiration. The force of the inspiratory act is, therefore, better adapted than that of the expiratory for testing the muscular strength of the body.

The following table expresses the result of numerous experiments by Mr. Hutchinson on this subject, the instrument used to gauge the inspiratory and expiratory power being a hæmadynamometer (see p. 164), to which was attached a tube fitting the nostrils, and through which the inspiratory or expiratory effort was made:—

Power of Inspiratory Muscles.		Power of Expiratory Muscles.
1·5 in.	Weak	2·0 in.
2·0 ,,	Ordinary	2·5 ,,
2·5 ,,	Strong	3·5 ,,
3·5 ,,	Very strong	4·5 ,,
4·5 ,,	Remarkable	5·8 ,,
5·5 ,,	Very remarkable	7·0 ,,
6·0 ,,	Extraordinary	8·5 ,,
7·0 ,,	Very extraordinary	10·0 ,,

Mr. Hutchinson remarks:—"Suppose a man to lift by his inspiratory muscles three inches of mercury, what muscular effort has he used? The mere quantity of fluid lifted may be very inconsiderable (and as such I have found men wonder they could not elevate more), but not

so the power exerted, when we recollect that hydrostatic law, which Mr. Bramah adopted to the construction of a very convenient press. To apply this law here, the diaphragm alone must act under such an effort, with a force equal to the weight of a column of mercury 3 inches in height, and whose base is commensurate to the area of the diaphragm. The area of the base of one of the chests now before the Society, is 57 square inches; therefore, had this man raised 3 inches of mercury by his inspiratory muscles, his diaphragm alone in this act must have opposed a resistance equal to more than 23 oz. on every inch of that muscle, and a total weight of more than 83 lbs. Moreover, the sides of his chest would resist a pressure from the atmosphere equal to the weight of a covering of mercury three inches in thickness, or more than 23 oz. on every inch surface, which, if we take at 318 square inches, the chest will be found resisting a pressure of 731 lbs.; and allowing the elastic resistance of the ribs as $1\frac{1}{2}$ inch of mercury, this will bring the weight resisted by the chest as follows:—

Diaphragm	83 lbs.
Walls of the chest	731 ,,
Elastic force	232 ,,
Total	1046

"In round numbers it may be said, that the parietes of the thorax resisted 1000 lbs. of atmospheric pressure, and that not counterbalanced,—to say nothing of the elastic power of the lungs, which co-operated with this pressure.

"I would not venture at present to state exactly the distribution of muscular fibre over the thorax, which is called into action when resisting this 1046 lbs., but I think I am safe in stating that nine-tenths of the thoracic surface conspire to this act.

"What is here said of the muscular part of the chest

resisting such a force, must not be confounded with a former statement of 'two-thirds being *lifted* by the inspiratory muscles, and one-third left dormant,' under a force equal to 301 lbs. In this case the 301 lbs. are *lifted*; in the other, nine-tenths of 1046 lbs. are said to be *resisted*.

"The glass receiver of an air-pump may *resist* 15 lbs. on the square inch, yet it may be said to *lift* nothing. This question of the thoracic muscular force and resistance, and muscular distribution, is rendered complicate by the presence of so much osseous matter entering into the composition of the chest, which can scarcely be considered to act the same as muscle."

The great force of the inspiratory efforts during apnœa was well shown in some of the experiments performed by the Medico-chirurgical Society's Committee on Suspended Animation. On inserting a glass tube into the trachea of a dog, and immersing the other end of the tube in a vessel of mercury, the respiratory efforts during apnœa were so great as to draw the mercury four inches up the tube. The influence of the same force was shown in other experiments, in which the heads of animals were immersed both in mercury and in liquid plaster of Paris. In both cases the material was found, after death, to have been drawn up into all the bronchial tubes, filling the tissue of the lungs.

Much of the force exerted in inspiration is employed in overcoming the resistance offered by the elasticity of the walls of the chest and of the lungs. Mr. Hutchinson estimated the amount of this elastic resistance, by observing the elevation of a column of mercury raised by the return of air forced, after death, into the lungs, in quantity equal to the known capacity of respiration during life; and he calculated that, in a man capable of breathing 200 cubic inches of air, the muscular power expended upon the elasticity of the walls of the chest, in making the deepest inspiration, would be equal to the raising of at least

301 pounds avoirdupois. To this must be added about 150 lbs. for the elastic resistance of the lungs themselves, so that the total force to be overcome by the muscles in the act of inspiring 200 cubic inches of air is more than 450 lbs.

In tranquil respiration, supposing the amount of breathing air to be twenty cubic inches, the resistance of the walls of the chest would be equal to lifting more than 100 pounds; and to this must be added about 70 pounds for the elasticity of the lungs. The elastic force overcome in ordinary inpiration must, therefore, be equal to about 170 pounds.

It is probable, that in the quiet ordinary respiration, which is performed without consciousness or effort of the will, the only forces engaged are those of the inspiratory muscles, and the elasticity of the walls of the chest and the lungs. It is not known under what circumstances the contractile power which the bronchial tubes possess, by means of their organic muscular fibres, is brought into action. It is possible, as Dr. R. Hall maintained, that it may exist in expiration; but it is more likely that its chief purpose is to regulate and adapt, in some measure, the quantity of air admitted to the lungs, and to each part of them, according to the supply of blood. Another purpose probably served by the muscular fibres of the bronchial tubes is that of contracting upon and gradually expelling collections of mucus, which may have accumulated within the tubes, and cannot be ejected by forced expiratory efforts, owing to collapse or other morbid conditions of the portion of lung proceeding from the obstructed tubes (Gairdner).

The muscular action in the lungs, morbidly excited, is probably the chief cause of the phenomena of spasmodic asthma. It may be demonstrated by galvanizing the lungs shortly after taking them from the body. Under such a stimulus, they contract so as to lift up water placed in a

tube introduced into the trachea (C. J. B. Williams); and Volkmann has shown that they may be made to contract by stimulating their nerves. He tied a glass tube, drawn fine at one end, into the trachea of a beheaded animal; and when the small end was turned to the flame of a candle, he galvanized the pneumogastric trunk. Each time he did so the flame was blown, and once it was blown out.

The changes of the air in the lungs effected by these respiratory movements are assisted by the various conditions of the air itself. According to the law observed in the diffusion of gases, the carbonic acid evolved in the air-cells will, independently of any respiratory movement, tend to leave the lungs, by diffusing itself into the external air, where it exists in less proportion; and according to the same law, the oxygen of the atmospheric air will tend of itself towards the air-cells in which its proportion is less than it is in the air in the bronchial tubes or in that external to the body. But for this tendency in the oxygen and carbonic acid to mix uniformly, within and without the lungs, the *reserve* and *residual* air would, probably, be very injuriously charged with carbonic acid; for the respiratory movements alone are not enough to empty the air cells, and perhaps expel only the air which lies in the larger bronchial tubes. Probably also the change is assisted by the different temperature of the air within and without the lungs; and by the action of the cilia on the mucous membrane of the bronchial tubes, the continual vibrations of which may serve to prevent the adhesion of the air to the moist surface of the membrane.

Movement of Blood in the Respiratory Organs.

To be exposed to the air thus alternately moved into and out of the air-cells and minute bronchial tubes, the blood is propelled from the right ventricle through the pulmonary

capillaries in steady streams, and slowly enough to permit every minute portion of it to be for a few seconds exposed to the air, with only the thin walls of the capillary vessels and air-cells intervening. The pulmonary circulation is of the simplest kind: for the pulmonary artery branches regularly; its successive branches run in straight lines, and do not anastomose; the capillary plexus is uniformly spread over the air-cells and intercellular passages; and the veins derived from it proceed in a course as simple and uniform as that of the arteries, their branches converging but not anastomosing. The veins have no valves, or only small imperfect ones prolonged from their angles of junction, and incapable of closing the orifice of either of the veins between which they are placed. The pulmonary circulation also is unaffected by changes of atmospheric pressure, and is not exposed to the influence of the pressure of muscles: the force by which it is accomplished, and the course of the blood are alike simple.

The blood which is conveyed to the lungs by the *pulmonary* arteries is distributed to these organs to be purified and made fit for the nutrition of all other parts of the body. The capillaries of the pulmonary vessels are arranged solely with reference to this object, and therefore can have but little to do with the *nutrition* of the lungs; or at least, only of those portions of the lungs with which they are in intimate connection for another purpose. For the nutrition of the rest of the lungs, including the pleura, interlobular tissue, bronchial tubes and glands, and the walls of the larger blood-vessels, a special supply of arterial blood is furnished through one or two *bronchial* arteries, the branches of which ramify in all these parts. The blood of the bronchial artery, when, having served for the nutrition of these parts, it has become venous, is carried partly into the branches of the bronchial vein, and thence to the *right* auricle, and partly into the small branches of the pulmonary artery, or, more directly, into the pulmonary

capillaries, whence, being with the rest of the blood arterialized, it is carried to the pulmonary veins and *left* side of the heart.

Changes of the Air in Respiration.

By their contact in the lungs the composition of both air and blood is changed. The alterations of the former being manifest, simpler than those of the latter, and in some degree illustrative of them, may be considered first.

The *atmosphere* we breathe has, in every situation in which it has been examined in its natural state, a nearly uniform composition. It is a mixture of oxygen, nitrogen, carbonic acid, and watery vapour, with, commonly, traces of other gases, as ammonia, sulphuretted hydrogen, etc. Of every 100 volumes of pure atmospheric air, 79 volumes (on an average) consist of nitrogen, the remaining 21 of oxygen. The proportion of carbonic acid is extremely small; 10,000 volumes of atmospheric air contain only about 4 or 5 of carbonic acid.

The quantity of watery vapour varies greatly, according to the temperature and other circumstances, but the atmosphere is never without some. In this country, the average quantity of watery vapour in the atmosphere is 1·40 per cent.

The changes produced by respiration on the atmospheric air are, that, 1, it is warmed; 2, its carbonic acid is increased; 3, its oxygen is diminished; 4, its watery vapour is increased; 5, a minute amount of organic matter and of free ammonia is added to it.

1. The expired air, heated by its contact with the interior of the lungs, is (at least in most climates) hotter than the inspired air. Its temperature varies between 97° and 99½°, the lower temperature being observed when the air has remained but a short time in the lungs, rather than when it is inhaled at a very low temperature; for whatever the temperature when inhaled may be, the air

nearly acquires that of the blood before it is expelled from the chest.

2. *The carbonic acid in respired air is always increased;* but the quantity exhaled in a given time is subject to change from various circumstances. From every volume of air inspired, about $4\frac{1}{2}$ per cent. of oxygen are abstracted; while a rather smaller quantity of carbonic acid is added in its place. It may be stated, as a general average deduced from the results of experiments by Valentin and Brunner, that, under ordinary circumstances, the quantity of carbonic acid exhaled into the air breathed by a healthy adult man amounts to 1346 cubic inches, or about 636 grains per hour. According to this estimate, which corresponds very closely with the one furnished by Sir H. Davy, and does not widely differ from those obtained by Allen and Pepys, Lavoisier, and Dr. Ed. Smith, the weight of carbon excreted from the lungs is about 173 grains per hour, or rather more than 8 ounces in the course of twenty-four hours. Discrepancies in the results obtained by different experimenters may be due to the variations to which the exhalation of carbonic acid is liable in different circumstances; for even in health the quantity varies according to age, sex, diversities in the respiratory movements, external temperature, the degree of purity of the respired air, and other circumstances. Each of these deserves a brief notice, because it affords evidence concerning either the sources of carbonic acid exhaled, or the mode in which it is separated from the blood.

a. Influence of Age and Sex.—According to Andral and Gavarret the quantity of carbonic acid exhaled into the air breathed by males, regularly increases from eight to thirty years of age; from thirty to forty it is stationary or diminishes a little; from forty to fifty the diminution is greater; and from fifty to extreme age it goes on diminishing, till it scarcely exceeds the quantity exhaled at ten years old. In females (in whom the quantity exhaled is

always less than in males of the same age) the same regular increase in quantity goes on from the eighth year to the age of puberty, when the quantity abruptly ceases to increase, and remains stationary so long as they continue to menstruate. When, however, menstruation has ceased, either in advancing years or in pregnancy, or morbid amenorrhœa, the exhalation of carbonic acid again augments; but when menstruation ceases naturally, it soon decreases again at the same rate that it does in old men.

b. Influence of Respiratory Movements.—According to Vierordt, the more quickly the movements of respiration are performed, the smaller is the proportionate quantity of carbonic acid contained in each volume of the expired air. Thus he found that, with six respirations per minute, the quantity of expired carbonic acid was 5·528 per cent.; with twelve respirations, 4·262 per cent.; with twenty-four, 3·355; with forty-eight, 2·984; and with ninety-six, 2·662. Although, however, the proportionate quantity of carbonic acid is thus diminished during frequent respiration, yet the absolute amount exhaled into the air within a given time is increased thereby, owing to the larger quantity of air which is breathed in the time. This is the case, whether the respiration be voluntarily accelerated, or naturally increased in frequency, as it is after feeding, active exercise, etc. By diminishing the frequency, and increasing the depth of respiration, the per-centage proportion of carbonic acid in the expired air is diminished; being in the deepest respiration as much as 1·97 per cent. less than in ordinary breathing. But for this proportionate diminution also, there is a full compensation in the greater total volume of air which is thus breathed. Finally, the last half of a volume of expired air contains more carbonic acid than the half first expired; a circumstance which is explained by the one portion of air coming from the remote part of the lungs, where it has been in more im-

mediate and prolonged contact with the blood than the other has, which comes chiefly from the larger bronchial tubes.

c. Influence of external Temperature.—The observations made by Vierordt at various temperatures between 38° F. and 75° F. show, for warm-blooded animals, that within this range, every rise equal to 10° F. causes a diminution of about two cubic inches in the quantity of carbonic acid exhaled per minute. Letellier, from experiments performed on animals at much higher and lower temperatures than the above, also found that the higher the temperature of the respired air (as far as 104° F.), the less is the amount of carbonic acid exhaled into it, whilst the nearer it approaches zero the more does the carbonic acid increase. The greatest quantity exhaled at the lower temperatures he found to be about twice as much as the smallest exhaled at the higher temperatures.

d. Season of the Year.—Dr. Edward Smith has shown that the season of the year, independently of temperature, also materially influences the respiratory phenomena; for with the same temperature, at different seasons, there is a great diversity in the amount of carbonic acid expired. According to his observations, spring is the season of the greatest, and autumn of the least activity of the respiratory and other functions.

e. Purity of the Respired Air.—The average quantity of carbonic acid given out by the lungs constitutes about 4·48 per cent. of the expired air; but if the air which is breathed be previously impregnated with carbonic acid (as is the case when the same air is frequently respired), then the quantity of carbonic acid exhaled becomes much less. This is shown by the results of two experiments performed by Allen and Pepys. In one, in which fresh air was taken in at each respiration, thirty-two cubic inches of carbonic acid were exhaled in a minute; whilst in the other, in which the same air was respired repeatedly, the quantity of carbonic

acid emitted in the same time was only 9·5 cubic inches. They found also that, however often the same air may be respired, even if until it will no longer sustain life, it does not become charged with more than ten per cent. of carbonic acid. The necessity of a constant supply of fresh air, by means of ventilation, through rooms in which many persons are breathing together, or in which, from any other source, much carbonic acid is evolved, is thus rendered obvious; for even when the air is not completely irrespirable, yet in the same proportion as it is already charged with carbonic acid, does the further extrication of that gas from the lungs suffer hindrance.

f. Hygrometric State of Atmosphere.—Lehmann's observations have shown that the amount of carbonic acid exhaled is considerably influenced by the degree of moisture of the atmosphere, much more being given off when the air is moist than when it is dry.

g. Period of the Day.—The *period of day* seems to exercise a slight influence on the amount of carbonic acid exhaled in a given time, though beyond the fact that the quantity exhaled is much less by night, we are scarcely yet in a position to state that variations in the amount exhaled occur at uniform periods of the day, independently of the influence of other circumstances.

h. Food.—By the *use of food* the quantity is increased, whilst by fasting it is diminished: and, according to Regnault and Reiset, it is greater when animals are fed on farinaceous food than when fed on meat. Spirituous drinks, especially when taken on an empty stomach, are generally believed to produce an immediate and marked diminution in the quantity of this gas exhaled. Recent observations by Dr. Edward Smith, however, furnish some singular results on this subject. Dr. Smith found, for example, that the effects produced by spirituous drinks depend much on the kind of drink taken. Pure alcohol tended rather to increase than to lessen respiratory changes, and the amount

therefore, of carbonic acid expired: rum, ale and porter, also sherry, had very similar effects. On the other hand, brandy, whisky and gin, particularly the latter, almost always lessened the respiratory changes, and consequently the amount of carbonic acid exhaled.

i. Exercise and Sleep.—Bodily exercise, in moderation, increases the quantity to about one-third more than it is during rest: and for about an hour after exercise, the volume of the air expired in the minute is increased about 118 cubic inches: and the quantity of carbonic acid about 7·8 cubic inches per minute. Violent exercise, such as full labour on the treadwheel, still further increases, according to Dr. E. Smith, the amount of the acid exhaled.

During *sleep*, on the other hand, there is a considerable diminution in the quantity of this gas evolved; a result probably in great measure dependent on the tranquillity of breathing: directly after walking, there is a great, though quickly transitory, increase in the amount exhaled. A larger quantity is exhaled when the barometer is low than when it is high.

3. *The Oxygen in respired Air is always less* than in the same air before respiration, and its diminution is generally proportionate to the increase of the carbonic acid. The experiments of Valentin and Brunner seem to show, that, for every volume of carbonic acid exhaled into the air, 1·17421 volumes of oxygen are absorbed from it: and that when the average quantity of carbonic acid, *i.e.*, 1346 cubic inches, or 636 grains, is exhaled in the hour, the quantity of oxygen absorbed in the same time is 1584 cubic inches or 542 grains. According to this estimate, there is more oxygen absorbed than is exhaled with carbon to form carbonic acid without change of volume; and to this general conclusion, namely, that the volume of air expired in a given time is less than that of the air inspired (allowance being made for the expansion in being heated), and that the loss is due to a portion of oxygen absorbed and not

returned in the exhaled carbonic acid, all observers agree, though as to the actual quantity of oxygen so absorbed, they differ even widely.

The quantity of oxygen that does not combine with the carbon given off in carbonic acid from the lungs, is probably disposed of in forming some of the carbonic acid and water given off from the skin, and in combining with sulphur and phosphorus to form part of the acids of the sulphates and phosphates excreted in the urine, and probably also, from the experiments of Dr. Bence Jones, with the nitrogen of the decomposing nitrogenous tissues.

The quantity of oxygen consumed seems to vary much, not only in different individuals, but in the same individual at different periods; thus it is considerably influenced by food, being greater in dogs when fed on farinaceous than on animal food, and much diminished during fasting, while it varies at different stages of digestion. Animals of small size consume a relatively much greater amount of oxygen than larger ones. The quantity of oxygen in the atmosphere surrounding animals, appears to have very little influence on the amount of this gas absorbed by them, for the quantity consumed is not greater even though an excess of oxygen be added to the atmosphere experimented with (Regnault and Reiset).

The Nitrogen of the Atmosphere, in relation to the respiratory process, is supposed to serve only mechanically, by diluting the oxygen, and moderating its action upon the system. This purpose, or the mode of expressing it, has been denied by Liebig, on the ground that if we suppose the nitrogen removed, the amount of oxygen in a given space would not be altered. But, although it be true that, if all the nitrogen of the atmosphere were removed and not replaced by any other gas, the oxygen might still extend over the whole space at present occupied by the mixture of which the atmosphere is composed; yet since, under ordinary circumstances, oxygen and nitrogen, when

mixed together in the ratio of one volume to four, produce a mixture which occupies precisely five volumes, with all the properties of atmospheric air, it must result that a given volume of atmosphere drawn into the lungs contains four-fifths less weight of oxygen than an equal volume composed entirely of oxygen. The greater rapidity and brilliancy with which combustion goes on in an atmosphere of oxygen than in one of common air, and the increased rapidity with which the ordinary effects of respiration are produced when oxygen instead of atmospheric air is breathed, seem to leave no doubt that the nitrogen with which the oxygen of the atmosphere is mixed has the effect of diluting this gas, in the same sense and degree as one part of alcohol is diluted when mixed with four parts of water.

It has been often discussed whether nitrogen is ever absorbed by or exhaled from the lungs during respiration.

At present, all that can be said on the subject is that, under most circumstances, animals appear to expire a very small quantity above that which exists in the inspired air. During prolonged fasting, on the contrary, a small quantity appears to be absorbed.

4. *Watery Vapour* is, under ordinary circumstances, always exhaled from the lungs in breathing. The quantity emitted is, as a general rule, sufficient to saturate the expired air, or very nearly so. Its absolute amount is, therefore, influenced by the following circumstances. First, by the quantity of air respired; for the greater this is, the greater also will be the quantity of moisture exhaled. Secondly, by the quantity of watery vapour contained in the air previous to its being inspired; because the greater this is, the less will be the amount required to complete the saturation of the air. Thirdly, by the temperature of the expired air; for the higher this is, the greater will be the quantity of watery vapour required to saturate the air. Fourthly, by the length of time which each volume

of inspired air is allowed to remain in the lungs; for it seems probable that, although during ordinary respiration the expired air is always saturated with watery vapour, yet when respiration is performed very rapidly the air has scarcely time to be raised to the highest temperature, or be fully charged with moisture ere it is expelled.

For ordinary cases, however, it may be held that the expired air is saturated with watery vapour, and hence is derivable a means of estimating the quantity exhaled in any given time: namely, by subtracting the quantity contained in the air inspired from the quantity which (at the barometric pressure) would saturate the same air at the temperature of expiration, which is ordinarily about 99°. And, on the other hand, if the quantity of watery vapour in the expired air be estimated, the quantity of air itself may from it be determined, being as much as that quantity of watery vapour would saturate at the ascertained temperature and barometric pressure.

The quantity of water exhaled from the lungs in twenty-four hours ranges (according to the various modifying circumstances already mentioned) from about 6 to 27 ounces, the ordinary quantity being about 9 or 10 ounces. Some of this is probably formed by the combination of the excess of oxygen absorbed in the lungs with the hydrogen of the blood; but the far larger proportion of it must be the mere exhalation of the water of the blood, taking place from the surfaces of the air-passages and cells, as it does from the free surfaces of all moist animal membranes, particularly at the high temperature of warm-blooded animals. It is exhaled from the lungs whatever be the gas respired, continuing to be expelled even in hydrogen gas.

5. The Rev. J. B. Reade showed, some years ago, and Dr. Richardson's experiments confirm the fact, that ammonia is among the ordinary constituents of expired air. It seems probable, however, both from the fact that this substance cannot be always detected, and from its minute

amount when present, that the whole of it may be derived from decomposing particles of food left in the mouth, or from carious teeth or the like; and that it is, therefore, only an accidental constituent of expired air.

The quantity of organic matter in the breath has been lately investigated by Dr. Ransome, who calculates that about 3 grains are given off from the lungs of an adult in twenty-four hours.

Changes produced in the Blood by Respiration.

The most obvious change which the blood undergoes in its passage through the lungs is that of *colour*, the dark crimson of venous blood being exchanged for the bright scarlet of arterial blood. (The circumstances which have been supposed to give rise to this change, the conditions capable of effecting it independent of respiration, and some other differences between arterial and venous blood, were discussed in the chapter on BLOOD, p. 85):—*2nd*, and in connection with the preceding change, it gains oxygen; *3rd*, it loses carbonic acid; *4th*, it becomes 1° or 2° F. warmer; *5th*, it coagulates sooner and more firmly, and, apparently, contains more fibrin.

The oxygen absorbed into the blood from the atmospheric air in the lungs is combined chemically with the hæmoglobin of the red blood corpuscles. In this condition it is carried in the arterial blood to the various parts of the body, and with it is, in the capillary system of vessels, brought into near relation or contact with the elementary parts of the tissues. Herein, co-operating probably in the process of nutrition, or in the removal of disintegrated parts of the tissues, a certain portion of the oxygen which the arterial blood contains disappears, and a proportionate quantity of carbonic acid and water is formed.

But it is not alone in the disintegrating processes to which all parts of the body are liable, that oxygen is consumed and carbonic acid and water are formed in its

consumption. A like process occurs in the blood itself, independently of the decay of the tissues; for on the continuance of such chemical processes depend, directly or indirectly, not only the temperature of the body, but all the forces, the nervous, the muscular, and others, manifested by the living organism.

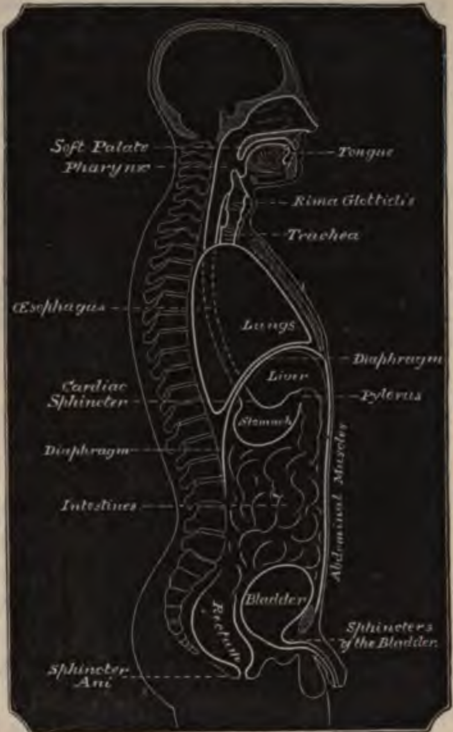
The venous blood, containing the new-formed carbonic acid, returns to the lungs, where a portion of the carbonic acid is exhaled, and a fresh supply of oxygen is again taken in.

Mechanism of Various Respiratory Actions.

It will be well here, perhaps, to explain some respiratory acts, which appear at first sight somewhat complicated, but cease to be so when the mechanism by which they are performed is clearly understood. The accompanying diagram (fig. 65) shows that the cavity of the chest is separated from that of the abdomen by the diaphragm, which, when acting, will lessen its curve, and thus descending, will push *downwards and forwards* the abdominal viscera; while the abdominal muscles have the opposite effect, and in acting will push the viscera *upwards and backward*, and with them the diaphragm, supposing its ascent to be not from any cause interfered with. From the same diagram it will be seen that the lungs communicate with the exterior of the body through the glottis, and further on through the mouth and nostrils — through either of them separately, or through both at the same time, according to the position of the soft palate. The stomach communicates with the exterior of the body through the œsophagus, pharynx, and mouth; while below, the rectum opens at the anus, and the bladder through the urethra. All these openings, through which the hollow viscera communicate with the exterior of the body, are guarded by muscles, called sphincters, which can

act independently of each other. The position of the latter is indicated in the diagram.

Fig. 65.



Let us take first the simple act of *sighing*. In this case there is a rather prolonged inspiratory effort by the diaphragm and other muscles concerned in inspiration; the air almost noiselessly passing in through the glottis, and by the elastic recoil of the lungs and chest-walls, and probably also of the abdominal walls, being rather suddenly expelled again.

Now, in the first, or *inspiratory* part of this act, the descent of the diaphragm presses the abdominal viscera downwards, and of course this pressure tends to evacuate the contents of such as communicate with the exterior of the body. Inasmuch, however, as their various openings are guarded by sphincter muscles, in a state of constant tonic contraction, there is no escape of their contents, and air simply enters the lungs. In the second, or *expiratory* part of the act of sighing, there is also pressure made

on the abdominal viscera in the opposite direction, by the elastic or muscular recoil of the abdominal walls; but the pressure is relieved by the escape of air through the open glottis, and the relaxed diaphragm is pushed up again into its original position. The sphincters of the stomach, rectum, and bladder act as before.

Hiccough resembles sighing in that it is an inspiratory act, but the inspiration is sudden instead of gradual, from the diaphragm acting suddenly and spasmodically; and the air, therefore, suddenly rushing through the unprepared rima glottidis, causes vibration of the vocal cords, and the peculiar sound.

In the act of *coughing*, there is most often first an inspiration, and this is followed by an expiration; but when the lungs have been filled by the preliminary inspiration, instead of the air being easily let out again through the glottis, the latter is momentarily closed by the approximation of the vocal cords; and then the abdominal muscles, strongly acting, push up the viscera against the diaphragm, and thus make pressure on the air in the lungs until its tension is sufficient to burst open noisily the vocal cords which oppose its outward passage. In this way a considerable force is exercised, and mucus or any other matter that may need expulsion from the lungs or trachea is quickly and sharply expelled by the out-streaming current of air.

Now it is evident on reference to the diagram (fig. 65), that pressure exercised by the abdominal muscles in the act of coughing, acts as forcibly on the abdominal viscera as on the lungs, inasmuch as the viscera form the medium by which the upward pressure on the diaphragm is made, and of necessity there is quite as great a tendency to the expulsion of their contents as of the air in the lungs. The instinctive and, if necessary, voluntarily increased contraction of the sphincters, however, prevents any escape at the openings guarded by them, and the pres-

sure is effective at one part only, namely, the rima glottidis.

The same remarks that apply to coughing, are almost exactly applicable to the act of *sneezing;* but in this instance the blast of air, on escaping from the lungs, is directed by an instinctive contraction of the pillars of the fauces and descent of the soft palate, chiefly through the nose, and any offending matter is thence expelled.

In the act of *vomiting,* as in coughing, there is first an inspiration; the glottis is then closed, and immediately afterwards the abdominal muscles strongly act; but here occurs the difference in the two actions. Instead of the vocal cords yielding to the action of the abdominal muscles, they remain tightly closed. Thus the diaphragm being unable to go up, forms an unyielding surface against which the stomach can be pressed. It is *fixed,* to use a technical phrase. At the same time the *cardiac* sphincter being relaxed while the *pylorus* is closed (see fig. 65), and the stomach itself also contracting, the action of the abdominal muscles, by these means assisted, expels the contents of the organ through the œsophagus, pharynx, and mouth. The reversed peristaltic action of the œsophagus probably increases the effect.

In the act of voluntary expulsion of urine or fæces, there is first an inspiration, as in coughing, sneezing, and vomiting; the glottis is then closed, and the diaphragm fixed as in vomiting. Now, however, both the rima glottidis and the cardiac opening of the stomach remain closed, and the sphincter of the bladder or rectum, or of both, being relaxed, the evacuation of the contents of these viscera takes place accordingly; the effect being, of course, increased by the muscular and elastic contraction of their own walls. As before, there is as much tendency to the escape of the contents of the lungs or stomach as of the rectum or bladder; but the pressure is relieved only at the orifice, the sphincter of which instinctively or involuntarily yields.

In all these expulsive actions the diaphragm is quite passive; and when it is *fixed*, it is in consequence of the closure of the glottis (which by preventing the exit of air from the lungs prevents its upward movement), not from any exertion on its own part.

In females, during parturition, almost an exactly similar action occurs, so far as the diaphragm and abdominal walls are concerned, to that which takes place in a straining effort at expulsion of urine or fæces. The contraction of the uterus, however, is both relatively and absolutely more powerful than that of the bladder or rectum, although it is greatly assisted by the inspiratory effort, by the fixing of the diaphragm, and by the action of the abdominal muscles, as in the other acts just described. In parturition, as in vomiting, the action of the abdominal muscles is, to a great extent, involuntary—more so than it commonly is in the expulsion of fæces or urine; but in these latter instances also, in cases of great pain and difficulty, it may cease to be a voluntary act, and be quite beyond the control of the will.

In *speaking*, there is a voluntary expulsion of air through the glottis by means of the abdominal muscles; and the vocal cords are put, by the muscles of the larynx, in a proper position and state of tension for vibrating as the air passes over them, and thus producing sound. The sound is moulded into words by the tongue, teeth, lips, etc.—the vocal cords producing the sound only, and having nothing to do with *articulation*.

Singing resembles speaking in the manner of its production; the laryngeal muscles, by variously altering the position and degree of tension of the vocal cords, producing the different notes. Words used in the act of singing are of course framed, as in speaking, by the tongue, teeth, lips, etc.

Sniffing is produced by a somewhat quick action of the diaphragm and other inspiratory muscles. The mouth is,

however, closed, and by these means the whole stream of air is made to enter by the nostrils. The alæ nasi are, commonly, at the same time, instinctively dilated.

Sucking is not properly a respiratory act, but it may be most conveniently considered in this place. It is caused chiefly by the depressor muscles of the os hyoides. These, by drawing downwards and backwards the tongue and floor of the mouth, produce a partial vacuum in the latter; and the weight of the atmosphere then acting on all sides tends to produce equilibrium on the inside and outside of the mouth as best it may. The communication between the mouth and pharynx is completely shut off, probably by the contraction of the pillars of the soft palate and descent of the latter so as to touch the back of the tongue; and the equilibrium, therefore, can be restored only by the entrance of something through the mouth. The action, indeed, of the tongue and floor of the mouth in sucking may be compared to that of the piston in a syringe, and the muscles which pull down the os hyoides and tongue, to the power which draws the handle.

In the preceding account of respiratory actions, the diaphragm and abdominal muscles have been, as the chief muscles engaged and for the sake of clearness, almost alone referred to. But, of course, in all *inspiratory* actions, the other muscles of inspiration (p. 195) are also more or less engaged; and in *expiration*, the abdominal muscles are assisted by others, previously enumerated (p. 199) as grouped in action with them.

Influence of the Nervous System in Respiration.

Like all other functions of the body, the discharge of which is necessary to life, respiration must be essentially an involuntary act. Else, life would be in constant danger, and would cease on the loss of consciousness for a few moments, even in sleep. But it is also necessary that respiration should be to some extent under the control of

the will. For were it not so, it would be impossible to perform those voluntary respiratory acts which have been just enumerated and explained, as speaking, singing, straining, and the like.

The respiratory movements and their regular rhythm, so far as they are involuntary and independent of consciousness (as on all ordinary occasions they are), seem to be under the absolute governance of the medulla oblongata, which, as a nervous centre, receives the impression of the "necessity of breathing," and reflects it to the phrenic and such other motor nerves as will bring into co-ordinate and adapted action the muscles necessary to inspiration.

In the cases of voluntary respiratory acts, we may believe that the brain, as well as the medulla oblongata, is engaged in the process; for we have no evidence of the mind exercising either perception or will through any other organ than the brain. But even when the brain is thus in action, it appears to be the medulla oblongata which combines the several respiratory muscles to act together. In such acts, for example as those of coughing and sneezing, the mind first perceives the irritation at the larynx or nose, and may exercise a certain degree of will in determining the actions, as *e.g.*, in the taking of the deep inspiration which always precedes them. But the mode in which the acts are performed, and the combination of muscles to effect them, are determined by the medulla oblongata, independently of the will, and have the peculiar character of reflex involuntary movements, in being always, and without practice or experience, precisely adapted to the end or purpose.

In these, and in all the other extraordinary respiratory actions, such as are seen in dyspnœa, or in straining, yawning, hiccough, and others, the medulla oblongata brings into adapted combination of action many other muscles besides those commonly exerted in respiration.

Almost all the muscles of the body, in violent efforts of dyspnœa, coughing, and the like, may be brought into action at once, or in quick succession; but more particularly the muscles of the larynx, face, scapula, spine, and abdomen co-operate in these efforts with the muscles of the chest. These, therefore, are often classed as secondary muscles of respiration; and the nerves supplying them, including especially the facial pneumogastric, spinal, accessory, and external respiratory nerves, were classed by Sir Charles Bell with the phrenic, as the respiratory system of nerves. There appears, however, no propriety in making a separate system of these nerves, since their mode of action is not peculiar, and many besides them co-operate in the respiratory acts. That which is peculiar in the nervous influence, directing the extraordinary movements of respiration, is, that so many nerves are combined towards one purpose by the power of a distinct nervous centre, the medulla oblongata. In other than respiratory movements, these nerves may act singly or together, without the medulla oblongata; but after it is destroyed, no movement adapted to respiration can be performed by any of the muscles, even though the part of the spinal cord from which they arise be perfect. The phrenic nerves, for example, are unable to excite respiratory movement of the diaphragm when their connection with the medulla oblongata is cut off, though their connection with the spinal cord may be uninjured.*

Effects of the Suspension and Arrest of Respiration.

These deserve some consideration, because of the illustration which they afford of the nature of the normal processes of respiration and circulation. When the process of respiration is stopped, either by arresting the respiratory move-

* The influence of the nervous system in respiration will be again and more particularly considered in the section treating of the medulla oblongata and pneumogastric nerves.

ments, or permitting them to continue in an atmosphere deprived of uncombined oxygen, the circulation of blood through the lungs is retarded, and at length stopped. The immediate effect of such retarded circulation is an obstruction to the exit of blood from the right ventricle: this is followed by delay in the return of venous blood to the heart; and to this succeeds venous congestion of the nervous centres and all the other organs of the body. In such retardation, also, an unusually small supply of blood is transmitted through the lungs to the left side of the heart; and this small quantity is venous.

The condition, then, in which a suffocated, or asphyxiated animal dies is, commonly, that the left side of the heart is nearly empty, while the lungs, right side of the heart, and other organs, are gorged with venous blood. To this condition many things contribute. *1st.* The obstructed passage of blood through the lungs, which appears to be the first of the events leading to suffocation, seems to depend on the cessation of the interchange of gases, as if blood charged with carbonic acid could not pass freely through the pulmonary capillaries. But the stagnation of blood in the pulmonary capillaries would not, perhaps, be enough to stop entirely the circulation, unless the action of the heart were also weakened. Therefore, *2ndly,* the fatal result is probably due, in some measure, to the enfeebled action of the right side of the heart, in consequence of its over-distension by blood continually flowing into it; this flow, probably, being much increased by the powerful but fruitless efforts continually made at inspiration (Eccles). And *3rdly,* because of the obstruction at the right side of the heart, there must be venous congestion in the medulla oblongata and nervous centres: and this evil is augmented by the left ventricle receiving and propelling none but venous blood. Hence, slowness and disorder of the respiratory movements and of the movements of the heart may be added. Under all these conditions combined, the

heart at length ceases to act; the cessation of its action being also in great measure, probably, brought about, *4thly*, by the imperfect supply of oxygenated blood to its muscular tissue.

In some experiments performed by a committee appointed by the Medico-Chirurgical Society to investigate the subject of Suspended Animation, it was found that, in the dog, during simple apnœa, *i.e.*, simple privation of air, as by plugging the trachea, the average duration of the respiratory movements after the animal had been deprived of air, was 4 minutes 5 seconds; the extremes being 3 minutes 30 seconds, and 4 minutes 40 seconds. The average duration of the heart's action, on the other hand, was 7 minutes 11 seconds; the extremes being 6 minutes 40 seconds, and 7 minutes 45 seconds. It would seem, therefore, that on an average, the heart's action continues for 3 minutes 15 seconds after the animal has ceased to make respiratory efforts. A very similar relation was observed in the rabbit. Recovery never took place after the heart's action had ceased.

The results obtained by the committee on the subject of drowning were very remarkable, especially in this respect, that whereas an animal may recover, after simple deprivation of air for nearly four minutes, yet, after submersion in water for 1½ minutes, recovery seems to be impossible. This remarkable difference was found to be due, not to the mere submersion, nor directly to the struggles of the animal, nor to depression of temperature, but to the two facts, that in drowning, a free passage is allowed to air out of the lungs, and a free entrance of water into them. In proof of the correctness of this explanation it was found that when two dogs of the same size, one, however, having his windpipe plugged, the other not, were submerged at the same moment, and taken out after being under water for 2 minutes, the former recovered on removal of the plug, the latter did not. It is probably to the entrance of water

into the lungs that the speedy death in drowning is mainly due. The results of *post-mortem* examination strongly support this view. On examining the lungs of animals deprived of air by plugging the trachea, they were found simply congested; but in the animals drowned, not only was the congestion much more intense, accompanied with ecchymosed points on the surface and in the substance of the lung, but the air tubes were completely choked up with a sanious foam, consisting of blood, water, and mucus, churned up with the air in the lungs by the respiratory efforts of the animal. The lung-substance, too, appeared to be saturated and sodden with water, which, stained slightly with blood, poured out at any point where a section was made. The lung thus sodden with water was heavy (though it floated), doughy, pitted on pressure, and was incapable of collapsing. It is not difficult to understand how, by such infarction of the tubes, air is debarred from reaching the pulmonary cells: indeed the inability of the lungs to collapse on opening the chest is a proof of the obstruction which the froth occupying the air-tubes offers to the transit of air. The entire dependence of the early fatal issue, in apnœa by drowning, upon the open condition of the windpipe, and its results, was also strikingly shown by the following experiment. A strong dog had its windpipe plugged, and was then submerged in water for four minutes; in three quarters of a minute after its release it began to breathe, and in four minutes had fully recovered. This experiment was repeated with similar results on other dogs. When the entrance of water into the lungs, and its drawing up with the air into the bronchial tubes by means of the respiratory efforts, were diminished, as by rendering the animal insensible by chloroform previously to immersion, and thus depriving it of the power of making violent respiratory efforts, it was found that it could bear immersion for a longer period without dying than when not thus rendered insensible. Probably to a like diminution

in the respiratory efforts, may also be ascribed the greater length of time persons have been found to bear submersion without being killed, when in a state of intoxication, poisoning by narcotics, or during insensibility from syncope.

It is to the accumulation of carbonic acid in the blood, and its conveyance into the organs, that we must, in the first place, ascribe the phenomena of asphyxia. For when this does not happen, all the other conditions may exist without injury; as they do, for example, in hybernating warm-blooded animals. In these, life is supported for many months in atmospheres in which the same animals, in their full activity, would be speedily suffocated. During the periods of complete torpor, their respiration almost entirely ceases; the heart acts very slowly and feebly; the processes of organic life are all but suspended, and the animal may be with impunity completely deprived of atmospheric air for a considerable period. Spallanzani kept a marmot, in this torpid state, immersed for four hours in carbonic acid gas, without its suffering any apparent inconvenience. Dr. Marshall Hall kept a lethargic bat under water for 16 minutes, and a lethargic hedgehog for $22\frac{1}{2}$ minutes; and neither of the animals appeared injured by the experiment.

CHAPTER VIII.

ANIMAL HEAT.

The average temperature of the human body in those internal parts which are most easily accessible, as the mouth and rectum, is from 98·5° to 99·5° F.

In different parts of the external surface of the human body the temperature varies only to the extent of two or three degrees, when all are alike protected from cooling

influences; and the difference which under these circumstances exists, depends chiefly upon the different degrees of blood-supply. In the arm-pit—the most convenient situation, under ordinary circumstances, for examination by the thermometer—the average temperature is 98·6° F.

The chief circumstances by which the temperature of the healthy body is influenced are the following:—

Age.—The average temperature of the new-born child is only about 1° F. above that proper to the adult; and the difference becomes still more trifling during infancy and early childhood. According to Wunderlich, the temperature falls to the extent of about $\frac{1}{5}$° to $\frac{1}{2}$° F. from early infancy to puberty, and by about the same amount from puberty to fifty or sixty years of age. In old age the temperature again rises, and approaches that of infancy.

Although the average temperature of the body, however, is not lower than that of younger persons, yet the power of resisting cold is less in them—exposure to a low temperature causing a greater reduction of heat than in young persons.

The same rapid diminution of temperature was observed by M. Edwards in the new-born young of most carnivorous and rodent animals when they were removed from the parent, the temperature of the atmosphere being between 50° and 53$\frac{1}{2}$° F.; whereas, while lying close to the body of the mother, their temperature was only 2 or 3 degrees lower than hers. The same law applies to the young of birds. Young sparrows, a week after they were hatched, had a temperature of 95° to 97°, while in the nest; but when taken from it, their temperature fell in one hour to 66$\frac{1}{2}$°, the temperature of the atmosphere being at the time 62$\frac{1}{2}$°. It appears from his investigations, that in respect of the power of generating heat, some Mammalia are born in a less developed condition than others; and that the young of dogs, cats, and rabbits, for example, are inferior to the young of those animals which are not born blind. The need of external warmth to keep up the temperature

of new-born children is well known; the researches of M. Edwards show, that the want of it is, as Hunter suggested, a much more frequent cause of death in new-born children than is generally supposed, and furnish a strong argument against the idea, that children, by early exposure to cold, can soon be hardened into resisting its injurious influence.

Sex.—The average temperature of the female would appear from observations by Dr. Ogle to be very slightly higher than that of the male.

Period of the Day.—The temperature undergoes a gradual alteration, to the extent of about 1° to 1½° F. in the course of the day and night; the *minimum* being at night or in the early morning, the *maximum* late in the afternoon.

Exercise.—*Active exercise* raises the temperature of the body. This may be partly ascribed to the fact, that every muscular contraction is attended by the development of one or two degrees of heat in the acting muscle; and that the heat is increased according to the number and rapidity of these contractions, and is quickly diffused by the blood circulating from the heated muscles. Possibly, also, some heat may be generated in the various movements, stretchings, and recoilings of the other tissues, as the arteries, whose elastic walls, alternately dilated and contracted, may give out some heat, just as caoutchouc alternately stretched and recoiling becomes hot. But the heat thus developed cannot be great.

Moreover, the increase of temperature throughout the whole body, produced by active exercise, is but small; the great apparent increase of heat depending, in a great measure, on the increased circulation and quantity of blood, and, therefore, greater heat, in parts of the body (as the skin, and especially the skin of the extremities), which, at the same time that they feel more acutely than others any changes of temperature are, under ordinary conditions, by some degrees colder than organs more centrally situated.

That the increased temperature of the skin during

exercise is not accompanied by a proportional increase of the heat of other parts, which are naturally much warmer, is well shown by some observations of Dr. J. Davy.

Climate and Season.—In passing from a temperate to a hot climate the temperature of the human body rises slightly, the increase rarely exceeding 2° to 3° F. In summer the temperature of the body is a little higher than in winter; the difference amounting to from $\frac{1}{5}$ to $\frac{1}{3}$° F. (Wunderlich).

The same effects are observable in alterations of temperature not depending on season or climate.

Food and Drink.—The effect of a meal upon the temperature of a body is but small. A very slight rise usually occurs.

Cold alcoholic drinks depress the temperature somewhat ($\frac{1}{2}$° to 1° F.). Warm alcoholic drinks, as well as warm tea and coffee, raise the temperature (about $\frac{1}{2}$° F.).

In disease the temperature of the body deviates from the normal standard to a greater extent than would be anticipated from the slight effect of external conditions during health. Thus, in some diseases, as pneumonia and typhus, it occasionally rises as high as 106° or 107° F.; and considerably higher temperatures have been noted. In a case of malignant fever recently recorded by Mr. Norman Moore, the temperature in the axilla rapidly rose to 111° F.; when the patient died. The highest temperature recorded in a living man, 112·5° F., was observed by Wunderlich, in a case of idiopathic tetanus, at the time of death. In the *morbus cæruleus*, in which there is defective arterialization of the blood from malformation of the heart, the temperature of the body may be as low as 79° or 77$\frac{1}{2}$°; in Asiatic cholera a thermometer placed in the mouth sometimes rises only to 77° or 79°; and in a case of tubercular meningitis, observed by Dr. Gee, the temperature of the rectum remained for hours at 79·4° F.

The temperature maintained by Mammalia in an active state of life, according to the tables of Tiedemann and

Rudolphi, averages 101°. The extremes recorded by them were 96° and 106°, the former in the narwhal, the latter in a bat (Vespertilio Pipistrella). In birds, the average is as high as 107°; the highest temperature, 111·25°, being in the small species, the linnets, etc. Among reptiles, Dr. John Davy found, that while the medium they were in was 75°, their average temperature was 82·5°. As a general rule, their temperature, though it falls with that of the surrounding medium, is, in temperate media, two or more degrees higher; and though it rises also with that of the medium, yet at very high degrees it ceases to do so, and remains even lower than that of the medium. Fish and Invertebrata present, as a general rule, the same temperature as the medium in which they live, whether that be high or low; only among fish, the tunny tribe, with strong hearts and red meat-like muscles, and more blood than the average of fish have, are generally 7° warmer than the water around them.

The difference, therefore, between what are commonly called the warm- and the cold-blooded animals, is not one of absolutely higher or lower temperature; for the animals which to us, in a temperate climate, feel cold (being like the air or water, colder than the surface of our bodies), would, in an external temperature of 100°, have nearly the same temperature and feel hot to us. The real difference is, as Mr. Hunter expressed it, that what we call warm-blooded animals (birds and Mammalia), have a certain "permanent heat in all atmospheres," while the temperature of the others, which we call cold-blooded, is "variable with every atmosphere."

The power of maintaining a uniform temperature, which Mammalia and birds possess, is combined with the want of power to endure such changes of temperature of their bodies as are harmless to the other classes; and when their power of resisting change of temperature ceases, they suffer serious disturbances or die.

Sources and Mode of Production of Heat in the Body.

In explaining the chemical changes effected in the process of respiration (p. 219), it was stated that the oxygen of the atmosphere taken into the blood is combined, in the course of the circulation, with the carbon and the hydrogen of disintegrated and absorbed tissues, and of certain elements of food which have not been converted into tissues. That such a combination between the oxygen of the atmosphere and the carbon and hydrogen in the blood, is continually taking place, is made certain by the fact, that a larger amount of carbon and hydrogen is constantly being added to the blood from the food than is required for the ordinary purposes of nutrition, and that a quantity of oxygen is also constantly being absorbed from the air in the lungs, of the disposal of which no account can be given except by regarding it as combining, for the most part, with the excess of carbon and hydrogen, and being excreted in the form of carbonic acid and water. In other words, the blood of warm-blooded animals appears to be always receiving from the digestive canal and the lungs more carbon, hydrogen, and oxygen than are consumed in the repair of the tissues, and to be always emitting carbonic acid and water, for which there is no other known source than the combination of these elements.* By such combination, heat is continually produced in the animal body. The same amount of heat will be evolved in the union of any given quantities of carbon and oxygen, and of hydrogen and oxygen, whether the combination be rapid and evident, as in ordinary combustion, or slow and imperceptible, as in the changes which occur in the living body. And since the heat thus arising will be generated wherever the blood

* Some heat will also be generated in the combination of sulphur and phosphorus with oxygen, to which reference has been made (p. 216); but the amount thus produced is but small.

is carried, every part of the body will be heated equally, or nearly so.

This theory, that the maintenance of the temperature of the living body depends on continual chemical change, chiefly by oxidation, of combustible materials existing in the tissues and in the blood, has long been established by the demonstration that the quantity of carbon and hydrogen which, in a given time, unites in the body with oxygen, is sufficient to account for the amount of heat generated in the animal within the same time: an amount capable of maintaining the temperature of the body at from 98° to 100°, notwithstanding a large loss by radiation and evaporation.

Many things observed in the economy and habits of animals are explicable by this theory, and may here briefly be quoted, although no longer required as additional evidence for its truth. Thus, as a general rule, in the various classes of animals, as well as in individual examples of each class, the quantity of heat generated in the body is in direct proportion to the activity of the respiratory process. The highest animal temperature, for example, is found in birds, in whom the function of respiration is most actively performed. In Mammalia, the process of respiration is less active, and the average temperature of the body less, than in birds. In reptiles, both the respiration and the heat are at a much lower standard; while in animals below them, in which the function of respiration is at the lowest point, a power of producing heat is, in ordinary circumstances, hardly discernible. Among these lower animals, however, the observations of Mr. Newport supply confirmatory evidence. He shows that the larva, in which the respiratory organs are smaller in comparison with the size of the body, has a lower temperature than the perfect insect. Volant insects have the highest temperature, and they have always the largest respiratory organs and breathe the greatest quantity of air; while among terrestrial insects, those also produce the most

heat which have the largest respiratory organs and breathe the most air. During sleep, hybernation, and other states of inaction, respiration is slower or suspended, and the temperature is proportionately diminished; while, on the other hand, when the insect is most active and respiring most voluminously, its amount of temperature is at its maximum, and corresponds with the quantity of respiration. Neither the rapidity of the circulation, nor the size of the nervous system, according to Mr. Newport, presents such a constant relation to the evolution of heat.

On the Regulation of the Temperature of the Human Body.

The continual production of heat in the body has been already referred to. There is also, of necessity, a continual loss. But in healthy warm-blooded animals, as already remarked, the loss and gain of heat are so nearly balanced one by the other, that under all ordinary circumstances, an uniform temperature, within two or three degrees, is preserved.

The loss of heat from the human body takes place chiefly by radiation and conduction from its surface, and by means of the constant evaporation of water from the same part, and from the air-passages. In each act of respiration, heat is also lost by so much warmth as the expired air acquires (p. 210). All food and drink which enter the body at a lower temperature than itself, abstract a small measure of heat, and the urine and fæces take about a like amount away, when they leave the body. Lastly, some part of the heat of the body is rendered imperceptible, and therefore lost as heat, by being manifested in the form of mechanical motion.

By far the most important loss of heat from the body,—probably 80 or 90 per cent. of the whole amount, is that which proceeds from radiation, conduction, and evaporation from the skin. And it is to this part especially, and in a smaller measure to the air-passages, that we must look

for the means by which the temperature is regulated; in other words, by which it is prevented from rising beyond the normal point on the one hand, or sinking below it on the other. The chief indirect means for accomplishing the same end are, variations in the amount and quality of the food and drink taken, variations in clothing, and in exposure to external heat or cold.

In order to understand the means by which the heat of the body is regulated, it is necessary to take into considération the following facts: First, the immediate source of heat in the body is the presence of a large quantity of a warm fluid—the blood, the temperature of which is, in health, about 100° F. In the second place, the blood, while constantly moving in a multitude of different streams, is, every minute or so, gathered up in the heart into one large stream, before being again dispersed to all parts of the body. In this way, the temperature of the blood remains almost exactly the same in all parts; for while a portion of it in passing through one organ, as the skin, may become cooler, and through another organ, as the liver, may become warmer, the effect on each separate stream is more or less neutralized when it mingles with another, and an average is struck, so to speak, for all the streams when they form one, in passing through the heart.

The means, by which the skin is able to act as one of the most important organs for regulating the temperature of the blood, are—(1), that it offers a large surface for radiation, conduction, and evaporation; (2), that it contains a large amount of blood; (3), that the quantity of blood contained in it is the greater under those circumstances which demand a loss of heat from the body, and *vice versâ*. For the circumstance which directly determines the quantity of blood in the skin, is that which governs the supply of blood to all the tissues and organs of the body, namely, the power of the vaso-motor nerves to cause

a greater or less tension of the muscular element in the walls of the arteries (see p. 141), and, in correspondence with this, a lessening or increase of the calibre of the vessel accompanied by a less or greater current of blood. A warm or hot atmosphere so acts on the nerve fibres of the skin, as to lead them to cause in turn a relaxation of the muscular fibre of the blood-vessels; and, as a result, the skin becomes full-blooded, hot, and sweating; and much heat is lost. With a low temperature, on the other hand, the blood-vessels shrink, and in accordance with the consequently diminished blood-supply, the skin becomes pale, and cold, and dry. Thus, by means of a self-regulating apparatus, the skin becomes the most important of the means by which the temperature of the body is regulated.

In connection with loss of heat by the skin, reference has been made to that which occurs both by radiation and conduction, and by evaporation; and the subject of animal heat has been considered almost solely with regard to the ordinary case of man living in a medium colder than his body, and therefore losing heat in all the ways mentioned. The importance of the means, however, adopted, so to speak, by the skin for regulating the temperature of the body, will depend on the conditions by which it is surrounded; an inverse proportion existing in most cases between the loss by radiation and conduction on the one hand, and by evaporation on the other. Indeed, the small loss of heat by evaporation in cold climates may go far to compensate for the greater loss by radiation; as, on the other hand, the great amount of fluid evaporated in hot air may remove nearly as much heat as is commonly lost by both radiation and evaporation in ordinary temperatures; and thus, it is possible, that the quantities of heat required for the maintenance of an uniform proper temperature in various climates and seasons are not so different as they, at first thought, seem.

Many examples might be given of the power which the

body possesses of resisting the effects of a high temperature, in virtue of evaporation from the skin.

Sir Charles Blagden and others supported a temperature varying between 198° and 211° F. in dry air for several minutes; and in a subsequent experiment he remained eight minutes in a temperature of 260°. But such heats are not tolerable when the air is moist as well as hot, so as to prevent evaporation from the body. M. C. James states, that in the vapour baths of Nero he was almost suffocated in a temperature of 112°, while in the caves of Testaccio, in which the air is dry, he was but little incommoded by a temperature of 176°. In the former, evaporation from the skin was impossible; in the latter, it was, probably, abundant, and the layer of vapour which would rise from all the surface of the body would, by its very slowly conducting power, defend it for a time from the full action of the external heat.

(The glandular apparatus, by which secretion of fluid from the skin is effected, will be considered in the Section on the Skin.)

The ways by which the skin may be rendered more efficient as a cooling-apparatus by exposure, by baths, and by other means, which man instinctively adopts for lowering his temperature when necessary, are too well known to need more than to be mentioned.

As a means for lowering the temperature, the lungs and air-passages are very inferior to the skin; although, by giving heat to the air we breathe, they stand next to the skin in importance. As a *regulating* power, the inferiority is still more marked. The air which is expelled from the lungs leaves the body at about the temperature of the blood, and is always saturated with moisture. No inverse proportion, therefore, exists between the loss of heat by radiation and conduction on the one hand, and by evaporation on the other. The colder the air, for example, the greater will be the loss in all ways. Neither

is the quantity of blood which is exposed to the cooling influence of the air diminished or increased, so far as is known, in accordance with any need in relation to temperature. It is true that by varying the number and depth of the respirations, the quantity of heat given off by the lungs may be made, to some extent, to vary also. But the respiratory passages, while they must be considered important means by which heat is lost, are altogether subordinate in the power of regulating the temperature, to the skin.

It may seem to have been assumed, in the foregoing pages, that the only regulating apparatus for temperature required by the human body is one that shall, more or less, produce a *cooling* effect; and as if the amount of heat produced were always, therefore, in excess of that which is required. Such an assumption would be incorrect. We have the power of regulating the production of heat, as well as its loss.

In *food* we have a means for elevating our temperature. It is the fuel, indeed, on which animal heat ultimately depends altogether. Thus, when more heat is wanted, we instinctively take more food, and take such kinds of it as are good for combustion; while everyday experience shows the different power of resisting cold possessed by the well-fed and by the starved.

In northern regions, again, and in the colder seasons of more southern climes, the quantity of food consumed is (speaking very generally) greater than that consumed by the same men or animals in opposite conditions of climate and seasons. And the food which appears naturally adapted to the inhabitants of the coldest climates, such as the several fatty and oily substances, abounds in carbon and hydrogen, and is fitted to combine with the large quantities of oxygen which, breathing cold dense air, they absorb from their lungs.

In exercise, again, we have an important means of raising the temperature of our bodies (p. 233).

The influence of *external coverings* for the body must not be unnoticed. In warm-blooded animals, they are always adapted, among other purposes, to the maintenance of uniform temperature; and man adapts for himself such as are, for the same purpose, fitted to the various climates to which he is exposed. By their means, and by his command over food and fire, he maintains his temperature on all accessible parts of the surface of the earth.

The *influence of the nervous system* in modifying the production of heat has been already referred to. The experiments and observations which best illustrate it are those showing, first, that when the supply of nervous influence to a part is cut off, the temperature of that part falls below its ordinary degree; and, secondly, that when death is caused by severe injury to, or removal of, the nervous centres, the temperature of the body rapidly falls, even though artificial respiration be performed, the circulation maintained, and to all appearance the ordinary chemical changes of the body be completely effected. It has been repeatedly noticed, that after division of the nerves of a limb, its temperature falls; and this diminution of heat has been remarked still more plainly in limbs deprived of nervous influence by paralysis. For example, Mr. Earle found the temperature of the hand of a paralysed arm to be 70°, while the hand of the sound side had a temperature of 92° F. On electrifying the paralysed limb, the temperature rose to 77°. In another case, the temperature of the paralysed finger was 56° F., while that of the unaffected hand was 62°.

With equal certainty, though less definitely, the influence of the nervous system on the production of heat, is shown in the rapid and momentary increase of temperature, sometimes general, at other times quite local, which is observed in states of nervous excitement; in the general increase of warmth of the body, sometimes amounting to perspiration, which is excited by passions of the mind; in

the sudden rush of heat to the face, which is not a mere sensation; and in the equally rapid diminution of temperature in the depressing passions. But none of these instances suffices to prove that heat is generated by mere nervous action, independent of any chemical change; all are explicable, on the supposition that the nervous system alters, by its power of controlling the calibre of the blood-vessels (p. 141), the quantity of blood supplied to a part; while any influence which the nervous system may have in the production of heat, apart from this influence on the blood-vessels, is an indirect one, and is derived from its power of causing nutritive change in the tissues, which may, by involving the necessity of chemical action, involve the production of heat. The existence of nerves, which regulate animal heat otherwise than by their influence in trophic (nutritive) or vaso-motor changes, although by many considered probable, is not yet proven.

In connection with the regulation of animal temperature, and its maintenance in health at the normal height, it is interesting to note the result of circumstances too powerful, either in raising or lowering the heat of the body, to be controlled by the proper regulating apparatus. Walther found that rabbits and dogs, when tied to a board and exposed to a hot sun, reached a temperature of 114·8° F., and then died. Cases of sunstroke furnish us with similar examples in the case of man; for it would seem that here death ensues chiefly or solely from elevation of the temperature. In a case related by Dr. Gee, the temperature in the axilla was 109·5° F.; and in many febrile diseases the immediate cause of death appears to be the elevation of the temperature to a point inconsistent with the continuance of life.

The effect of mere loss of bodily temperature in man is less well known than the effect of heat.

From experiments by Walther, it appears that rabbits can be cooled down to 48° F. before they die, if artificial

respiration be kept up. Cooled down to 64° F., they cannot recover unless external warmth be applied together with the employment of artificial respiration. Rabbits not cooled below 77° F. recover by external warmth alone.

CHAPTER IX.

DIGESTION.

Digestion is the process by which those parts of our food which may be employed in the formation and repair of the tissues, or in the production of heat, are made fit to be absorbed and added to the blood.

Food.

Food may be considered in its relation to these two purposes—the nutrition of the tissues, and the production of heat. But, under the first of these heads will be included many other allied functions, as, for example, secretion and generation: and under the second, not the production of heat only as such, but of all the other forces correlated with it, which are manifested by the living body.

The following is a convenient tabular classification of the usual and more necessary kinds of food:—

Nitrogenous:—

Proteids, as Albumen, Casein, Syntonin, Gluten, and their allies, and Gelatin; (containing Carbon, Hydrogen, Oxygen, and Nitrogen; some of them, also Sulphur and Phosphorus).

Non-Nitrogenous:—

(1). Amyloids—Starch, Sugar, and their allies (containing Carbon, Hydrogen and Oxygen).

(2). Oils and Fats (containing Carbon, Hydrogen, and Oxygen; the oxygen in much smaller proportion than in starch or sugar).

(3). Mineral or Saline Matters; as Chloride of Sodium, Phosphate of Lime, etc.

(4). Water.

Animals cannot subsist on any but organic substances, and these must contain the several elements and compounds which are naturally combined with them: in other words, not even organic compounds are nutritive unless they are supplied in their natural state. Pure fibrin, pure gelatin, and other principles purified from the substances naturally mingled with them, are incapable of supporting life for more than a brief time.

Moreover, health cannot be maintained by any number of substances derived exclusively from one only of the two chief groups of alimentary principles mentioned above. A mixture of nitrogenous and non-nitrogenous organic substances, together with the inorganic principles which are severally contained in them, is essential to the well-being, and, generally, even to the existence of an animal. The truth of this is demonstrated by experiments performed for the purpose, and is illustrated by the composition of the food prepared by nature, as the exclusive source of nourishment to the young of Mammalia, namely, milk.

COMPOSITION OF MILK.

	Human.	Cows.
Water	890	858
Solids	110	142
	1,000	1,000
Casein	35	68
Butter	25	38
Sugar (with extractives)	48	30
Salts	2	6
	110	142

In milk, as will be seen from the preceding table, the albuminous group of aliments is represented by the casein, the oleaginous by the butter, the aqueous by the water, the saccharine by the sugar of milk. Among the salts of milk are likewise phosphate of lime, alkaline, and other salts, and a trace of iron; so that it may be briefly said

to include all the substances which the tissues of the growing animal need for their nutrition, and which are required for the production of animal heat.

The yelk and albumen of eggs are in the same relation as food for the embryoes of oviparous animals, that milk is to the young of Mammalia, and afford another example of mixed food being provided as the most perfect nutrition.

COMPOSITION OF FOWLS' EGGS.

	White.		Yelk.
Water	80·0		53·73
Albumen	15·5		17·47
Mucus	4·5	Yellow Oil	28·75
Salts	4·0		6·0

Experiments illustrating the same principle have been performed by Magendie and others. Dogs were fed exclusively on sugar and distilled water. During the first seven or eight days they were brisk and active, and took their food and drink as usual; but in the course of the second week, they began to get thin, although their appetite continued good, and they took daily between six and eight ounces of sugar. The emaciation increased during the third week, and they became feeble, and lost their activity and appetite. At the same time an ulcer formed on each cornea, followed by an escape of the humours of the eye: this took place in repeated experiments. The animals still continued to eat three or four ounces of sugar daily; but became at length so feeble as to be incapable of motion, and died on a day varying from the thirty-first to the thirty-fourth. On dissection, their bodies presented all the appearances produced by death from starvation; indeed, dogs will live almost the same length of time without any food at all.

When dogs were fed exclusively on gum, results almost similar to the above ensued. When they were kept on olive-oil and water, all the phenomena produced were the same, except that no ulceration of the cornea took place:

the effects were also the same with butter. Tiedemann and Gmelin obtained very similar results. They fed different geese, one with sugar and water, another with gum and water, and a third with starch and water. All gradually lost weight. The one fed with gum died on the sixteenth day; that fed with sugar, on the twenty-second; the third, which was fed with starch, on the twenty-fourth; and another on the twenty-seventh day; having lost, during these periods, from one-sixth to one-half of their weight. The experiments of Chossat and Letellier prove the same; and in men, the same is shown by the various diseases to which they who consume but little nitrogenous food are liable, and especially, as Dr. Budd has shown, by the affection of the cornea which is observed in Hindus feeding almost exclusively on rice. But it is not only the non-nitrogenous substances, which, taken alone, are insufficient for the maintenance of health. The experiments of the Academies of France and Amsterdam were equally conclusive that gelatin alone soon ceases to be nutritive.

Mr. Savory's observations on food confirm and extend the results obtained by Magendie, Chossat, and others. They show that animals fed exclusively on non-nitrogenous diet speedily emaciate and die, as if from starvation; that a much larger amount of urine is voided by those fed with nitrogenous than by those with non-nitrogenous food; and that animal heat is maintained as well by the former as by the latter—a fact which proves that nitrogenous elements of food, as well as non-nitrogenous, may be regarded as calorifacient. The non-nitrogenous principles, however, he believes to be calorifacient essentially, not being first converted into tissue; but of the nitrogenous, he believes that only a part is thus directly calorifacient, the rest being employed in the formation of tissue. Contrary to the views of Liebig and Lehmann, Savory has shown that, while animals speedily die when confined to non-nitro-

genous diet, they may live long when fed exclusively with nitrogenous food.

Man is supported as well by food constituted wholly of animal substances, as by that which is formed entirely of vegetable matters, on the condition, of course, that it contain a mixture of the various nitrogenous and non-nitrogenous substances just shown to be essential for healthy nutrition. In the case of carnivorous animals, the food upon which they exist, consisting as it does of the flesh and blood of other animals, not only contains all the elements of which their own blood and tissues are composed, but contains them combined, probably, in the same forms. Therefore, little more may seem requisite, in the preparation of this kind of food for the nutrition of the body, than that it should be dissolved and conveyed into the blood in a condition capable of being re-organized. But in the case of the herbivorous animals, which feed exclusively upon vegetable substances, it might seem as if there would be greater difficulty in procuring food capable of assimilation into their blood and tissues. But the chief ordinary articles of vegetable food contain substances identical in composition, with the albumen, fibrin, and casein, which constitute the principal nutritive materials in animal food. Albumen is abundant in the juices and seeds of nearly all vegetables; the gluten which exists, especially in corn and other seeds of grasses as well as in their juices, is identical in composition with fibrin, and is often named vegetable fibrin; and the substance named legumen, which is obtained especially from peas, beans, and other seeds of leguminous plants, and from the potato, is identical with the casein of milk. All these vegetable substances are, equally with the corresponding animal principles, and in the same manner, capable of conversion into blood and tissue; and as the blood and tissues in both classes of animals are alike, so also the nitrogenous food of both may be regarded as, in essential respects, similar.

It is in the relative quantities of the nitrogenous and non-nitrogenous compounds in these different foods that the difference lies, rather than in the presence of substances in one of them which do not exist in the other. The only non-nitrogenous compounds in ordinary animal food are the fat, the saline matters, and water, and, in some instances, the vegetable matters which may chance to be in the digestive canals of such animals as are eaten whole. The amount of these, however, is altogether much less than that of the non-nitrogenous substances represented by the starch, sugar, gum, oil, etc., in the vegetable food of herbivorous animals.

The effects of total deprivation of food have been made the subject of experiments on the lower animals, and have been but too frequently illustrated in man.

(1). One of the most notable effects of starvation, as might be expected, is loss of weight; the loss being greatest at first, as a rule, but afterwards not varying very much, day by day, until death ensues. Chossat found that the ultimate proportional loss was, in different animals experimented on, almost exactly the same; death occurring when the body had lost two-fifths (forty per cent.) of its original weight.

Different parts of the body lose weight in very different proportions. The following results are taken, in round numbers, from the table given by M. Chossat:—

Fat loses	93	per cent.
Blood	75	,,
Spleen	71	,,
Pancreas	64	,,
Liver	52	,,
Heart	44	,,
Intestines	42	,,
Muscles of locomotion	42	,,
Stomach loses	39	,,

Pharynx, Œsophagus	34	per cent.
Skin	33	,,
Kidneys	31	,,
Respiratory apparatus	22	,,
Bones	16	,,
Eyes	10	,,
Nervous system	2	,, (nearly).

(2). The effect of starvation on the temperature of the various animals experimented on by Chossat was very marked. For some time the *variation* in the daily temperature was more marked than its absolute and continuous diminution, the daily fluctuation amounting to 5° or 6° F., instead of 1° or 2° F., as in health. But a short time before death, the temperature fell very rapidly, and death ensued when the loss had amounted to about 30° F. It has been often said, and with truth, although the statement requires some qualification, that death by starvation is really death by cold; for not only has it been found that differences of time with regard to the period of the fatal result are attended by the same ultimate loss of heat, but the effect of the application of external warmth to animals cold and dying from starvation, is more effectual in reviving them than the administration of food. In other words, an animal exhausted by deprivation of nourishment is unable so to digest food as to use it as fuel, and therefore is dependent for heat on its supply from without. Similar facts are often observed in the treatment of exhaustive diseases in man.

(3). The symptoms produced by starvation in the human subject are hunger, accompanied, or it may be replaced, by pain, referred to the region of the stomach; insatiable thirst; sleeplessness; general weakness and emaciation. The exhalations both from the lungs and skin are fœtid, indicating the tendency to decomposition which belongs to badly-nourished tissues; and death occurs, sometimes after the additional exhaustion caused by diarrhœa, often

with symptoms of nervous disorder, delirium, or convulsions.

(4). In the human subject death commonly occurs within six to ten days after total deprivation of food. But this period may be considerably prolonged by taking a very small quantity of food, or even water only. The cases so frequently related of survival after many days, or even some weeks, of abstinence, have been due either to the last-mentioned circumstances, or to others less effectual, which prevented the loss of heat and moisture. Cases in which life has continued after total abstinence from food and drink for many weeks, or months, exist only in the imagination of the vulgar.

(5). The appearances presented after death from starvation are those of general wasting and bloodlessness, the latter condition being least noticeable in the brain. The stomach and intestines are empty and contracted, and the walls of the latter usually appear remarkably thinned and almost transparent. The usual secretions are scanty or absent, with the exception of the bile, which, somewhat concentrated, usually fills the gall-bladder. All parts of the body readily decompose.

It has just been remarked that man can live upon animal matters alone, or upon vegetables. The structure of his teeth, however, as well as experience, seems to declare that he is best fitted for a mixed diet; and the same inference may be readily gathered from other facts and considerations. Thus, the food a man takes into his body daily, represents or ought to represent the quantity and kind of matter necessary for replacing that which is daily cast out by the way of lungs, skin, kidneys, and other organs. To find out, therefore, the quantity and kind of food necessary for a healthy man, it will, evidently, be the best plan to consider in the first place what he loses by excretion.

For the sake of example, we may now take only two elements, carbon and nitrogen, and, if we discover what amount of these is respectively discharged in a given time from the body, we shall be in a position to judge what kind of food will most readily and economically replace their loss.

The quantity of carbon daily lost from the body amounts to about 4,500 grains, and of nitrogen 300 grains; and if a man could be fed by these elements, as such, the problem would be a very simple one; a corresponding weight of charcoal, and, allowing for the oxygen in it, of atmospheric air, would be all that is necessary. But, as before remarked, an animal can live only upon these elements when they are arranged in a particular manner with others, in the form of an organic compound, as albumen, starch, and the like; and the relative proportion of carbon to nitrogen in either of these compounds alone, is, by no means, the proportion required in the diet of man. The amount, 4,500 grains of carbon, represents about fifteen times the quantity of nitrogen required in the same period; and, in albumen, the proportion of carbon to nitrogen is only as 3·5 to 1. If therefore, a man took into his body, as food, sufficient albumen to supply him with the needful amount of carbon, he would receive more than four times as much nitrogen as he wanted; and if he took only sufficient to supply him with nitrogen, he would be starved for want of carbon. It is plain, therefore, that he should take with the albuminous part of his food, which contains so large a relative amount of nitrogen in proportion to the carbon he needs, substances in which the nitrogen exists in much smaller quantities.

Food of this kind is provided in such compounds as starch and fat. The latter indeed as it exists for the most part in considerable amount mingled with the flesh of animals, removes to a great extent, in a diet of animal

food, the difficulty which would otherwise arise from a deficiency of carbon—fat containing a large relative proportion of this element, and no nitrogen.

To take another example; the proportion of carbon to nitrogen in bread is about 30 to 1. If a man's diet were confined to bread, he would eat, therefore, in order to obtain the requisite quantity of nitrogen, twice as much carbon as is necessary; and it is evident, that, in this instance, a certain quantity of a substance with a large relative amount of nitrogen is the kind of food necessary for redressing the balance.

To place the preceding facts in a tabular form, and taking meat as an example instead of pure albumen:—meat contains about 10 per cent. of carbon, and rather more than 3 per cent. of nitrogen. Supposing a man to take meat for the supply of the needful carbon, he would require 45,000 grains, or nearly 6½ lbs, containing:—

Carbon	4,500 grains
Nitrogen	1,350 ,,
Excess of Nitrogen above the amount required	1,500 ,,

Bread contains about 30 per cent. of carbon and 1 per cent. of nitrogen.

If bread alone, therefore, were taken as food, a man would require, in order to obtain the requisite nitrogen, 30,000 grains, containing—

Carbon	9,000 grains
Nitrogen	300 ,,
Excess of Carbon above the amount required .	4,500 ,,

But a combination of bread and meat would supply much more economically what was necessary. Thus—

	Carbon.	Nitrogen.
15,000 grains of bread (or rather more than 2lb.) contain	4,500 grs.	150 grs.
5,000 grains of meat (or about ¾lb.) contain .	500 ,,	150 ,,
	5,000 ,,	300 ,,

So that $\frac{3}{4}$ lb. of meat, and less than 2 lbs. of bread would supply all the needful carbon and nitrogen with but little waste.

From these facts it will be plain that a mixed diet is the best and most economical food for man; and the result of experience entirely coincides with what might have been anticipated on theoretical grounds only.

It must not be forgotten, however, that the value of certain foods may depend quite as much on their digestibility, as on the relative quantities of the necessary elements which they contain.

In actual practice, moreover, the quantity and kind of food to be taken with most economy and advantage cannot be settled for each individual, only by considerations of the exact quantities of certain elements that are required. Much will of necessity depend on the habits and digestive powers of the individual, on the state of his excretory organs, and on many other circumstances. Food which to one person is appropriate enough, may be quite unfit for another; and the changes of diet so instinctively practised by all to whom they are possible, have much more reliable grounds of justification than any which could be framed on theoretical considerations only.

In many of the experiments on the digestibility of various articles of food, disgust at the sameness of the diet may have had as much to do with inability to consume and digest it, as the want of nutritious properties in the substances which were experimented on. And that disease may occur from the want of particular food, is well shown by the occurrence of scurvy when fresh vegetables are deficient, and its rapid cure when they are again eaten: and the disease which is here so remarkably evident in its symptoms, causes, and cure, is matched by numberless other ailments, the causes of which, however, although analogous, are less exactly known, and therefore less easily combated.

With regard to the quantity, too, as well as the kind of food necessary, there will be much diversity in different individuals. Dr. Dalton believed, from some experiments which he performed, that the quantity of food necessary for a healthy man, taking free exercise in the open air, is as follows:—

Meat	16 ounces,	or 1·00 lb.	avoird.
Bread	19 ,,	,, 1·19 ,,	,,
Butter or Fat	$3\frac{1}{2}$,,	,, 0·22 ,,	,,
Water	52 fluid ozs.	,, 3·38 ,,	,,

The quantity of meat, however, here given is probably more in proportion to the other articles of diet enumerated than is needful for the majority of individuals under the circumstances stated.

PASSAGE OF FOOD THROUGH THE ALIMENTARY CANAL.

The course of the food through the alimentary canal of man will be readily seen from the accompanying diagram (fig. 66). The food taken into the mouth passes thence through the œsophagus into the stomach, and from this into the small and large intestine successively; gradually losing, by absorption, the greater portion of its nutritive constituents. The residue, together with such matters as may have been added to it in its passage, is discharged from the rectum through the anus.

We shall now consider, in detail, the process of digestion, as it takes place in each stage of this journey of the food through the alimentary canal.

The Salivary Glands and the Saliva.

The first of a series of changes to which the food is subjected in the digestive canal, takes place in the cavity of the mouth; the solid articles of food are here submitted to the action of the teeth (p. 59), whereby they are divided

salivary glands, and the mucus secreted by the lining membrane of the whole buccal cavity.

The glands concerned in the production of *saliva*, are very extensive, and, in man and Mammalia generally, are presented in the form of four pairs of large glands, the parotid, submaxillary, sublingual, and numerous smaller bodies, of similar structure and with separate ducts, which are scattered thickly beneath the mucous membrane of the lips, cheeks, soft palate, and root of the tongue. The structure of all these glands is essentially the same. Each is composed of several parts, called *lobes*, which are joined together by areolar tissue; and each of these lobes, again, is made up of a number of smaller parts called *lobules*, bound together as before by areolar tissue. Each of these small divisions, called lobules, is a miniature representation of the whole gland. It contains a small branch of the duct, which, subdividing, ends in small vesicular pouches, called *acini*, a group of which may be considered the

Fig. 67.*

dilated end of one of the smaller ducts (fig. 67). Each of the acini is about $\frac{1}{500}$ of an inch in diameter, and is formed of a fine structureless membrane, lined on the inner surface and often filled by spheroidal or glandular epithelium;

* Fig. 67. Diagram of a racemose or saccular compound gland; *m*, entire gland, showing branched duct and lobular structure; *n*, a lobule detached, with *o*, branch of duct proceeding from it (after Sharpey).

while on the outside there is a plexus of capillary blood-vessels. The accompanying diagram is intended to show the typical structure of such glands as the salivary (fig. 67).

Saliva, as it commonly flows from the mouth, is mixed with the secretion of the mucous membrane, and often with air bubbles, which, being retained by its viscidity, make it frothy.

When obtained from the parotid ducts, and free from mucus, saliva is a transparent watery fluid, the specific gravity of which varies from 1·004 to 1·008, and in which, when examined with the microscope, are found floating a number of minute particles, derived from the secreting ducts and vesicles of the glands. In the impure or mixed saliva are found, besides these particles, numerous epithelial scales separated from the surface of the mucous membrane of the mouth and tongue, and mucus-corpuscles, discharged for the most part from the tonsils, which, when the saliva is collected in a deep vessel, and left at rest, subside in the form of a white opaque matter, leaving the supernatant salivary fluid transparent and colourless, or with a pale bluish-grey tint. In *reaction*, the saliva, when first secreted, appears to be always alkaline; and that from the parotid gland is said to be more strongly alkaline than that from the other salivary glands. This alkaline condition is most evident when digestion is going on, and according to Dr. Wright, the degree of alkalinity of the saliva bears a direct proportion to the acidity of the gastric fluid secreted at the same time. During fasting, the saliva, although secreted alkaline, shortly becomes neutral; and it does so especially when secreted slowly and allowed to mix with the acid mucus of the mouth, by which its alkaline reaction is neutralized.

The following analysis of the saliva is by Frerichs:—

Composition of Saliva.

Water	994·10
Solids	5·90
Ptyalin	1·41
Fat	0·07
Epithelium and Mucus	2·13
Salts:—	
Sulpho-Cyanide of Potassium	
Phosphate of Soda	
,, ,, Lime	2·29
,, ,, Magnesia	
Chloride of Sodium	
,, ,, Potassium	
	5·90

The rate at which saliva is secreted is subject to considerable variation. When the tongue and muscles concerned in mastication are at rest, and the nerves of the mouth are subject to no unusual stimulus, the quantity secreted is not more than sufficient, with the mucus, to keep the mouth moist. But the flow is much accelerated when the movements of mastication take place, and especially when they are combined with the presence of food in the mouth. It may be excited also, even when the mouth is at rest, by the mental impressions produced by the sight or thought of food; also by the introduction of food into the stomach. The influence of the latter circumstance was well shown in a case mentioned by Dr. Gairdner, of a man whose pharynx had been divided: the injection of a meal of broth into the stomach was followed by the secretion of from six to eight ounces of saliva.

Under these varying circumstances, the *quantity* of saliva secreted in twenty-four hours varies also; its average amount is probably from two to three pints in twenty-four hours. In a man who had a fistulous opening of the parotid duct, Mitscherlich found that the quantity of saliva discharged from it during twenty-four hours, was from two

to three ounces; and the saliva collected from the mouth during the same period, and derived from the other salivary glands, amounted to six times more than that from the one parotid.

The *purposes served by saliva* are of several kinds. In the first place, acting mechanically in conjunction with mucus, it keeps the mouth in a due condition of moisture, facilitating the movements of the tongue in speaking, and the mastication of food. (2.) It serves also in dissolving sapid substances, and rendering them capable of exciting the nerves of taste. But the principal mechanical purpose of the saliva is, (3) that by mixing with the food during mastication, it makes it a soft pulpy mass, such as may be easily swallowed. To this purpose the saliva is adapted both by quantity and quality. For, speaking generally, the quantity secreted during feeding is in direct proportion to the dryness and hardness of the food: as M. Lassaigne has shown, by a table of the quantity produced in the mastication of a hundred parts of each of several kinds of food, thirty parts suffice for a hundred parts of crumb of bread, but not less than 120 for the crusts; 42·5 parts of saliva are produced for the hundred of roast meat; 3·7 for as much of apples; and so on, according to the general rule above stated. The quality of saliva is equally adapted to this end. It is easy to see how much more readily it mixes with most kinds of food than water alone does; and M. Bernard has shown that the saliva from the parotid, labial, and other small glands, being more aqueous than the rest, is that which is chiefly *braided* and mixed with the food in mastication; while the more viscid mucoid secretion of the submaxillary, palatine, and tonsillitic glands is spread over the surface of the softened mass, to enable it to slide more easily through the fauces and œsophagus. This view obtains confirmation from the interesting fact pointed out by Professor Owen, that in the great ant-eater, whose enormously elongated tongue is kept moist by a large quantity

of viscid saliva, the submaxillary glands are remarkably developed, while the parotids are not of unusual size.

Beyond these, its mechanical purposes, saliva performs (4) a chemical part in the digestion of the food. When saliva, or a portion of a salivary gland, or even a portion of dried *ptyalin*, is added to starch paste, the starch is very rapidly transformed into dextrin and grape-sugar; and when common raw starch is masticated and mingled with saliva, and kept with it at a temperature of 90° or 100°, the starch-grains are cracked or eroded, and their contents are transformed in the same manner as the starch-paste. Changes similar to these are effected on the starch of farinaceous food (especially after cooking) in the stomach; and it is reasonable to refer them to the action of the saliva, because the acid of the gastric fluid tends to retard or prevent, rather than favour the transformation of the starch. It may therefore be held, that one purpose served by the saliva in the digestive process is that of assisting in the transformation of the starch, which enters so largely into the composition of most articles of vegetable food, and which (being naturally insoluble) is converted into soluble dextrin and grape-sugar, and made fit for absorption.

Besides saliva, many azotized substances, especially if in a state of incipient decomposition, may excite the transformation of starch, such as pieces of the mucous membrane of the mouth, bladder, rectum, and other parts, various animal and vegetable tissues, and even morbid products; but the gastric fluid will not produce the same effect. The transformation in question is effected much more rapidly by saliva, however, than by any of the other fluids or substances experimented with, except the pancreatic secretion, which, as will be presently shown, is very analogous to saliva. The actual process by which these changes are effected is still obscure. Probably the azotized substance, *ptyalin*, acts as a kind of ferment, like diastase

in the process of malting, and excites molecular changes in the starch which result in its transformation, first into dextrin and then into sugar.

The majority of observers agree that the transformation of starch into sugar ceases on the entrance of the food into the stomach, or on the addition of gastric fluid to it in a test-tube: while others maintain that it still goes on. Probably all are right: for, although gastric fluid added to saliva appears to arrest the action of the latter on starch, yet portions of saliva mingled with food in mastication may, for some time after their entrance into the stomach, remain unneutralized by the gastric secretion, and continue their influence upon the starchy principles in contact with them.

Starch appears to be the only principle of food upon which saliva acts chemically: it has no apparent influence on any of the other ternary principles, such as sugar, gum, cellulose, or (according to Bernard) on fat, and seems to be equally destitute of power over albuminous and gelatinous substances, so that we have as yet no information respecting any purpose it can serve in the digestion of Carnivora, beyond that of softening or macerating the food; though, since such animals masticate their food very little, usually "bolting" it, the saliva has probably but little use even in this respect, in the process of digestion.

Passage of Food into the Stomach.

When properly masticated, the food is transmitted in successive portions to the stomach by the act of *deglutition* or *swallowing*. This act, for the purpose of description, may be divided into three parts. In the first, particles of food collected to a morsel glide between the surface of the tongue and the palatine arch, till they have passed the anterior arch of the fauces; in the second, the morsel is carried through the pharynx; and in the third, it reaches the stomach through the œsophagus. These three acts

follow each other rapidly. The first is performed voluntarily by the muscles of the tongue and cheeks. The second also is effected with the aid of muscles which are in part endued with voluntary motion, such as the muscles of the soft palate and pharynx; but it is, nevertheless, an involuntary act, and takes place without our being able to prevent it, as soon as a morsel of food, drink, or saliva is carried backwards to a certain point of the tongue's surface. When we appear to swallow voluntarily, we only convey, through the first act of deglutition, a portion of food or saliva beyond the anterior arch of the palate; then the substance acts as a stimulus, which, in accordance with the laws of reflex movements hereafter to be described, is carried by the sensitive nerves to the medulla oblongata, when it is reflected by the motor nerves, and an involuntary adapted action of the muscles of the palate and pharynx ensues. The third act of deglutition takes place in the œsophagus, the muscular fibres of which are entirely beyond the influence of the will.

The second act of deglutition is the most complicated, because the food must pass by the posterior orifice of the nose and the upper opening of the larynx without touching them. When it has been brought, by the first act, between the anterior arches of the palate, it is moved onwards by the tongue being carried backwards, and by the muscles of the anterior arches contracting on it and then behind it. The root of the tongue being retracted, and the larynx being raised with the pharynx and carried forwards under the tongue, the epiglottis is pressed over the upper opening of the larynx, and the morsel glides past it; the closure of the glottis being additionally secured by the simultaneous contraction of its own muscles: so that, even when the epiglottis is destroyed, there is little danger of food or drink passing into the larynx so long as its muscles can act freely. At the same time the raising of the soft palate, so that its posterior edge touches the back part of the pharynx, and

the approximation of the sides of the posterior palatine arch, which move quickly inwards like side curtains, close the passage into the upper part of the pharynx and the posterior nares, and form an inclined plane, along the under surface of which the morsel descends; then the pharynx, raised up to receive it, in its turn contracts, and forces it onwards into the œsophagus.

In the third act, in which the food passes through the œsophagus, every part of that tube as it receives the morsel and is dilated by it, is stimulated to contract: hence an undulatory contraction of the œsophagus, which is easily observable in horses while drinking, proceeds rapidly along the tube. It is only when the morsels swallowed are large, or taken too quickly in succession, that the progressive contraction of the œsophagus is slow, and attended with pain. Division of both pneumogastric nerves paralyzes the contractile power of the œsophagus, and food accordingly accumulates in the tube (Bernard).

DIGESTION OF FOOD IN THE STOMACH.

Structure of the Stomach.

It appears to be an almost universal character of animals, that they have an internal cavity for the production of a chemical change in the aliment—a cavity for digestion; and when this cavity is compound, the part in which the food undergoes its principal and most important changes is the stomach.

In man and those Mammalia which are provided with a single stomach, its walls consist of three distinct layers or coats, viz., an external peritoneal, an internal mucous, and an intermediate muscular coat, with blood-vessels, lymphatics, and nerves distributed in and between them.

The *muscular coat* of the stomach consists of three separate layers or sets of fibres, which, according to their several directions, are named the longitudinal, circular, and oblique. The *longitudinal* set are the most superficial: they are con-

tinuous with the longitudinal fibres of the œsophagus, and spread out in a diverging manner over the great end and sides of the stomach. They extend as far as the pylorus, being especially distinct at the lesser or upper curvature of the stomach, along which they pass in several strong bands. The next set are the *circular* or *transverse* fibres, which more or less completely encircle all parts of the stomach; they are most abundant at the middle and in the pyloric portion of the organ, and form the chief part of the thick projecting ring of the pylorus. According to Pettigrew, these fibres are not simple circles, but form double or figure-of-8 loops, the fibres intersecting very obliquely. The next, and consequently deepest set of fibres, are the *oblique*, continuous with the circular muscular fibres of the œsophagus, and, according to Pettigrew, with the same double-looped arrangement that prevails in the preceding layer: they are comparatively few in number, and are placed only at the cardiac orifice and portion of the stomach, over both surfaces of which they are spread, some passing obliquely from left to right, others from right to left, around the cardiac orifice, to which, by their interlacing, they form a kind of sphincter, continuous with that around the lower end of the œsophagus. The fibres of which the several muscular layers of the stomach, and of the intestinal canal generally, are composed, belong the class of *organic* muscle, being composed of smooth or unstriped, elongated, spindle-shaped fibre-cells; a fuller description of which will be given under the head of Muscular Tissue.

The *mucous membrane* of the stomach, which rests upon a layer of loose cellular membrane, or submucous tissue, is smooth, level, soft, and velvety; of a pale pink colour during life, and in the contracted state is thrown into numerous, chiefly longitudinal, folds or rugæ, which disappear when the organ is distended.

In its general structure the mucous membrane of the stomach resembles that of other parts (See Structure of Mucous Membrane.) But there are certain peculiarities

shared with the mucous membrane of the small and large intestines, which, doubtless, are connected with the peculiar functions, especially those relating to absorption, which these parts of the alimentary canal perform.

Entering largely into the construction of the mucous membrane, especially in the superficial part of the *corium*, is a quantity of a very delicate kind of connective tissue, called *retiform* tissue (fig. 72), or sometimes *lymphoid* or *adenoid* tissue, because it so closely resembles that which forms the stroma, or supporting framework of lymphatic glands (see Section on Lymphatic Glands); the resemblance being made much closer by the fact that the interspaces of this retiform tissue are filled with corpuscles not to be distinguished from lymph-corpuscles.

At the deepest part of the mucous membrane, is a layer of unstriped muscular fibres, called the *muscularis mucosæ*, which must not be confounded with the layers of muscle constituting the proper muscular coat, and from which it is separated by the submucous tissue. The *muscularis mucosæ* is found in the œsophagus, as well as in the stomach and intestines.

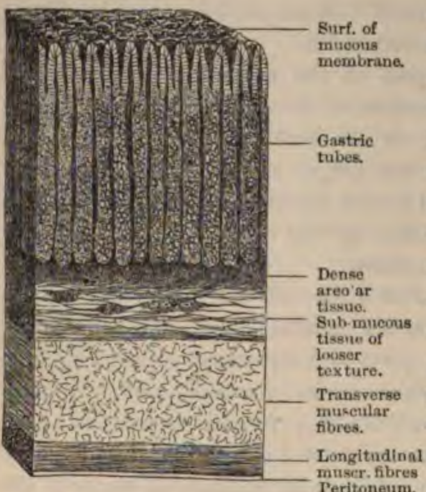
When examined with a lens, the internal or free surface of the stomach presents a peculiar honeycomb appearance, produced by shallow polygonal depressions or cells (fig. 68), the diameter of which varies generally from $\frac{1}{200}$th to $\frac{1}{350}$th of an inch; but near the pylorus is as much as $\frac{1}{100}$th of an inch. They are separated by slightly elevated ridges, which sometimes, especially in certain morbid states of the stomach, bear minute, narrow, vascular processes, which look like villi, and have given rise to the erroneous supposition that the stomach has absorbing villi, like those of the small intestines. In the bottom of the cells minute openings are visible (fig. 68), which are the orifices of perpendicularly arranged tubular glands (fig. 69), imbedded side by side in sets or bundles, in the substance of the mucous membrane, and composing nearly the whole structure.

The glands which are found in the human stomach may be divided into two classes, the *tubular* and *lenticular*.

Fig. 68.*

Tubular glands. The tubular glands may be described as a collection of cylinders with blind extremities, about $\frac{1}{25}$th of an inch in length, and $\frac{1}{350}$ in diameter, packed closely together, with their long axis at right angles to the surface of the mucous membrane on which they open, their blind ends resting on the submucous tissue. (See fig. 69). They are all composed of basement membrane, and lined by epithelial cells, but they are not all of exactly similar shape; for while some are simple straight tubes, open at one end and closed at the other (fig. 69), others present at their deeper extremities a varicose, pouched, or in some cases, even a branched appearance (fig. 70, *b* and *c*). The

Fig. 69.†

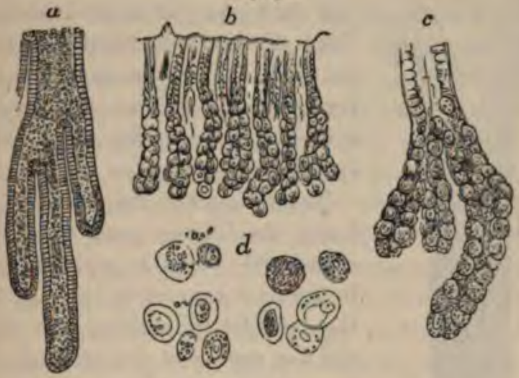


* Fig. 68. Small portion of the surface of the mucous membrane of the stomach (from Ecker) $\frac{20}{1}$.—The specimen shows the shallow depressions, in each of which the smaller dark spots indicate the orifices of a variable number of the gastric tubular glands.

† Fig. 69. Portion of human stomach (magnified 30 diameters) cut vertically, both in a direction *parallel* to its long axis, and *across* it (altered from Brinton).

epithelium lining them is not the same throughout. In the upper third or fourth of their length it is cylindrical,

Fig. 70.[*]



and continuous with that which covers the free mucous surface of the rest of the stomach. In their lower part, on the other hand, it is of the variety called glandular or spheroidal, the cells being oval or somewhat angular, and about $\frac{1}{1200}$th of an inch in diameter. The cells, however, do not completely fill up the cavity of the gland which they line, but leave a slight, central, thread-like space, the immediate lining of which is a layer of small angular cells, continuous with the cylindrical epithelium in the upper portion of the tube. This description will become plain on reference to fig. 71, which represents on a larger scale a longitudinal section of one of the glands depicted in fig. 69.

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[*] Fig. 70. The gastric glands of the human stomach (magnified). *a*, deep part of a pyloric gastric gland (from Kölliker); the cylindrical epithelium is traceable to the cæcal extremities. *b*, and *c*, cardiac gastric glands (from Allen Thompson); *b* vertical section of a small portion of the mucous membrane with the glands magnified 30 diameters; *c*, deeper portion of one of the glands, magnified 65 diameters, showing a slight division of the tubes, and a sacculated appearance, produced by the large glandular cells within them; *d*, cellular elements of the cardiac glands magnified 250 diameters.

In the greater number of the glands which are branched at their deeper extremities, the spheroidal epithelium exists in the divisions, while the main duct and the upper part of the branches are lined by the cylindrical variety (fig. 70, *c*). In the human stomach, according to Dr. Brinton, the simple undivided tubes are the rule, and the *branched* the exception.

Fig. 71.*

The varieties in the epithelial cells lining the different parts of the tubes, correspond probably with differences in the fluid secreted by their agency—the cylinder-epithelium, like that on the free surface of the stomach, being probably engaged in separating the thin alkaline mucus which is always present in greater or less quantity, while the larger glandular cells probably secrete the proper gastric juice.

Near the pylorus there exist glands branched at their deep extremities, which are lined throughout by cylinder-epithelium (fig. 70, *a*), and probably serve only for the secretion of mucus.

All the tubular glands, while they open by one end into the cavity of the stomach, rest by their blind extremities on a bed or matrix of areolar tissue (fig. 69), which is prolonged upwards between them, so as to invest and support them.

Lenticular glands.—Besides the cylindrical glands, there

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* Fig. 71. Part of one of the gastric glands, highly magnified, to show the arrangement of the epithelium in its interior; *a*, columnar cells lining the upper part of the tube: *b*, small angular cells, into which these merge below to form a central or axial layer within; *c*, the proper gastric or glandular cells (after Brinton).

are also small closed sacs beneath the surface of the mucous membrane, resembling exactly the *solitary* glands of the intestine, to be described hereafter. Their number is very variable, and they are found chiefly along the lesser curvature of the stomach, and in the pyloric region, but they may be present in any part of the organ. According to Dr. Brinton they are rarely absent in children. Their function probably resembles that of the intestinal solitary glands, but nothing is certainly known regarding it.

The blood-vessels of the stomach, which first break up in the submucous tissue, send branches upward between the closely packed glandular tubes, anastomosing around them by means of a fine capillary network with oblong meshes. Continuous with this deeper plexus, or prolonged upwards from it, so to speak, is a more superficial network of larger capillaries, which branch densely around the orifices of the tubes, and form the framework on which are moulded the small elevated ridges of mucous membrane bounding the minute, polygonal pits before referred to. From this *superficial* network the veins chiefly take their origin. Thence passing down between the tubes, with no very free connection with the deeper *inter-tubular* capillary plexus, they open finally into the venous network in the submucous tissue.

The nerves of the stomach are derived from the pneumogastric and sympathetic.

Secretion and Properties of the Gastric Fluid.

While the stomach contains no food, and is inactive, no gastric fluid is secreted; and mucus, which is either neutral or slightly alkaline, covers its surface. But immediately on the introduction of food or other foreign substance into the stomach, the mucous membrane, previously quite pale, becomes slightly turgid and reddened with the influx of a larger quantity of blood; the gastric glands commence secreting actively, and an acid fluid is poured

out in minute drops, which gradually run together and flow down the walls of the stomach, or soak into the substances introduced. The *quantity* of this fluid secreted daily has been variously estimated; but the average for a healthy adult has been assumed to range from ten to twenty pints in the twenty-four hours (Brinton).

The first accurate analysis of the *gastric fluid* was made by Dr. Prout: but it does not appear that it was collected in any large quantity, or pure and separate from food, until the time when Dr. Beaumont was enabled, by a fortunate circumstance, to obtain it from the stomach of a man named St. Martin, in whom there existed, as the result of a gunshot wound, an opening leading directly into the stomach, near the upper extremity of the great curvature, and three inches from the cardiac orifice. The external opening was situate two inches below the left mamma, in a line drawn from that part to the spine of the left ilium. The borders of the opening into the stomach, which was of considerable size, had united, in healing, with the margins of the external wound, but the cavity of the stomach was at last separated from the exterior by a fold of mucous membrane, which projected from the upper and back part of the opening, and closed it like a valve, but could be pushed back with the finger. The introduction of any mechanical irritant, such as the bulb of a thermometer, into the stomach, excited at once the secretion of gastric fluid. This could be drawn off with a caoutchouc tube, and could often be obtained to the extent of nearly an ounce. The introduction of alimentary substances caused a much more rapid and abundant secretion of pure gastric fluid than the presence of other mechanical irritants did. No increase of temperature could be detected during the most active secretion; the thermometer introduced into the stomach always stood at 100° Fahr., except during muscular exertion, when the temperature of the stomach, like

that of other parts of the body, rose one or two degrees higher.

M. Blondlot, and subsequently M. Bernard, and since then, several others, by maintaining fistulous openings into the stomachs of dogs, have confirmed most of the facts discovered by Dr. Beaumont. And the man St. Martin has frequently submitted to renewed experiments on his stomach, by various physiologists. From all these observations it appears, that pepper, salt, and other soluble stimulants, excite a more rapid discharge of gastric fluid than mechanical irritation does; so do alkalies generally, but acids have a contrary effect. When mechanical irritation is carried beyond certain limits so as to produce pain, the secretion, instead of being more abundant, diminishes or ceases entirely, and a ropy mucus is poured out instead. Very cold water, or small pieces of ice, at first render the mucous membrane pallid, but soon a kind of reaction ensues, the membrane becomes turgid with blood, and a larger quantity of gastric juice is poured out. The application of too much ice is attended by diminution in the quantity of fluid secreted, and by consequent retardation of the process of digestion. The quantity of the secretion seems to be influenced also by impressions made on the mouth; for Blondlot found that when sugar was introduced into the dog's stomach, either alone, or mixed with human saliva, a very small secretion ensued: but when the dog had himself masticated and swallowed it, the secretion was abundant.

Dr. Beaumont described the secretion of the human stomach as "a clear transparent fluid, inodorous, a little saltish, and very perceptibly acid. Its taste is similar to that of thin mucilaginous water, slightly acidulated with muriatic acid. It is readily diffusible in water, wine, or spirits; slightly effervesces with alkalies; and is an effectual solvent of the *materia alimentaria*. It possesses the

property of coagulating albumen in an eminent degree; is powerfully antiseptic, checking the putrefaction of meat; and effectually restorative of healthy action, when applied to old fœtid sores and foul ulcerating surfaces."

The chemical composition of the gastric juice of the human subject has been particularly investigated by Schmidt, a favourable case for his doing so occurring in the person of a peasant named Catherine Kütt, aged 35, who for three years had had a gastric fistula under the left mammary gland, between the cartilages of the ninth and tenth ribs.

The fluid was obtained by putting into the stomach some hard indigestible matter, as dry peas, and a little water, by which means the stomach was excited to secretion, at the same time that the matter introduced did not complicate the analysis by being digested in the fluid secreted. The gastric juice was drawn off through an elastic tube inserted into the fistula.

The fluid thus obtained was acid, limpid, and odourless, with a mawkish taste. Its density varied from 1·0022 to 1·0024. Under the microscope a few cells from the gastric glands and some fine granular matter were observable.

The following table gives the mean of two analyses of the above-mentioned fluid; and arranged by the side of it, for purposes of comparison, is an analysis of gastric juice from the sheep and dog.

Composition of Gastric Juice.

		Human Gastric Juice.	Sheep's Gastric Juice.	Dog's Gastric Juice.
Water		994·40	986·14	971·17
Solid Constituents		5·59	13·85	28·82
Solids	Ferment, Pepsin (with a trace of Ammonia)	3·19	4·20	17·50
	Hydrochloric Acid	0·20	1·55	2·70
	Chloride of Calcium	0·06	0·11	1·66
	,, Sodium	1·46	4·36	3·14
	,, Potassium	0·55	1·51	1·07
	Phosphate of Lime, Magnesia, and Iron	0·12	2·09	2·73

In all the above analyses the amount of water given must be reckoned as rather too much, inasmuch as a certain quantity of saliva was mixed with the gastric fluid. The allowance, however, to be made on this account is only very small.

Considerable difference of opinion has existed concerning the nature of the free acid contained in the gastric juice, chiefly whether it is *hydrochloric* or *lactic*. The weight of evidence, however, is in favour of free hydrochloric acid, being that to which, in the human subject, the acidity of the gastric fluid is mainly due; although there is no doubt that others, as lactic, acetic, butyric, are not unfrequently to be found therein.

The *animal matter* mentioned in the analysis of the gastric fluid is named *pepsin*, from its power in the process of digestion. It is an azotised substance, and is best procured by digesting portions of the mucous membrane of the stomach in cold water, after they have been macerated for some time in water at a temperature between 80° and 100° F. The warm water dissolves various substances as well as some of the pepsin, but the cold water takes up little else than pepsin, which, on evaporating the cold

solution, is obtained in a greyish-brown viscid fluid. The addition of alcohol throws down the pepsin in greyish-white flocculi; and one part of the principle thus prepared, if dissolved in even 60,000 parts of water, will digest meat and other alimentary substances.

The *digestive power of the gastric fluid* is manifested in its softening, reducing into pulp, and partially or completely dissolving various articles of food placed in it at a temperature of from 90° to 100°. This, its peculiar property, requires the presence of both the pepsin and the acid; neither of them can digest alone, and when they are mixed, either the decomposition of the pepsin, or the neutralization of the acid, at once destroys the digestive property of the fluid. For the perfection of the process also, certain conditions are required, which are all found in the stomach; namely (1), a temperature of about 100° F.; (2), such movements as the food is subjected to by the muscular actions of the stomach, which bring in succession every part of it in contact with the mucous membrane, whence the fresh gastric fluid is being secreted; (3), the constant removal of those portions of food which are already digested, so that what remains undigested may be brought more completely into contact with the solvent fluid; and (4) a state of softness and minute division, such as that to which the food is reduced by mastication previous to its introduction into the stomach.

The chief circumstances connected with the mode in which the gastric fluid acts upon food during natural digestion, have been determined by watching its operations when removed from the stomach and placed in conditions as nearly as possible like those under which it acts while within that viscus. The fact that solid food, immersed in gastric fluid out of the body, and kept at a temperature of about 100°, is gradually converted into a thick fluid similar to chyme, was shown by Spallanzani, Dr. Stevens, Tiedemann and Gmelin and others. They used the gastric fluid

of dogs, obtained by causing the animals to swallow small pieces of sponge, which were subsequently withdrawn, soaked with the fluid—and proved nearly as much as the latter experiments of the same kind of gastric fluid by Blondlot, Bernard and others. But these need not be particularly referred to, while we have the more satisfactory and instructive observations which Dr. Beaumont made with the fluid obtained from the stomach of St. Martin. After the man had fasted seventeen hours, Dr. Beaumont took one ounce of gastric fluid, put into it a solid piece of boiled recently salted beef weighing three drachms, and placed the vessel which contained them in a water-bath heated to 100°. "In forty minutes digestion had distinctly commenced over the surface of the meat; in fifty minutes, the fluid had become quite opaque and cloudy, the external texture began to separate and become loose; and in sixty minutes chyme began to form. At 1 p.m." (two hours after the commencement of the experiment) "the cellular texture seemed to be entirely destroyed, leaving the muscular fibres loose and unconnected, floating about in small fine shreds, very tender and soft." In six hours, they were nearly all digested—a few fibres only remaining. After the lapse of ten hours, every part of the meat was completely digested. The gastric juice, which was at first transparent, was now about the colour of whey, and deposited a fine sediment of the colour of meat. A similar piece of beef was, at the time of the commencement of this experiment, suspended in the stomach by means of a thread: at the expiration of the first hour it was changed in about the same degree as the meat digested artificially; but at the end of the second hour, it was completely digested and gone.

In other experiments, Dr. Beaumont withdrew through the opening of the stomach some of the food which had been taken twenty minutes previously, and which was completely mixed with the gastric juice. He continued

the digestion, which had already commenced, by means of artificial heat in a water-bath. In a few hours the food thus treated was completely chymified; and the artificial seemed in this, as in several other experiments, to be exactly similar to, though a little slower than, the natural digestion.

The apparent identity of the process in- and outside of the stomach thus manifested, while it shows that we may regard digestion as essentially a chemical process, when once the gastric fluid is formed, justifies the belief that Dr. Beaumont's other experiments with the digestive fluid may exactly represent the modifications to which, under similar conditions, its action in the stomach would be liable. He found that, if the mixture of food and gastric fluid were exposed to a temperature of 34° F., the process of digestion was completely arrested. In another experiment, a piece of meat which had been macerated in water at a temperature of 100° for several days, till it acquired a strong putrid odour, lost, on the addition of some fresh gastric juice, all signs of putrefaction, and soon began to be digested. From other experiments he obtained the data for estimates of the degrees of digestibility of various articles of food, and of the ways in which the digestion is liable to be affected, to which reference will again be made.

When natural gastric juice cannot be obtained, many of these experiments may be performed with an *artificial digestive fluid*, the action of which, probably, very closely resembles that of the fluid secreted by the stomach. It is made by macerating in water portions of fresh or recently dried mucous membrane of the stomach of a pig * or other omnivorous animal, or of the fourth stomach of the calf,

* The best portion of the stomach of the pig for this purpose is that between the cardiac and pyloric orifices; the cardiac portion appears to furnish the least active digestive fluid.

and adding to the infusion a few drops of hydrochloric acid—about 3·3 grains to half an ounce of the mixture, according to Schwann. Portions of food placed in such fluid, and maintained with it at a temperature of about 100°, are, in an hour or more, according to the toughness of the substance, softened and changed in just the same manner as they would be in the stomach.

The nature of the action by which the mucous membrane of the stomach and its secretion work these changes in organic matter is exceedingly obscure. The action of the pepsin may be compared with that of a ferment, which at the same time that it undergoes change itself, induces certain changes also in the organic matters with which it is in contact. Or its mode of action may belong to that class of chemical processes termed "catalytic," in which a substance excites, by its mere presence, and without itself undergoing change as ordinary ferments do, some chemical action in the substances with which it is in contact. So, for example, spongy platinum, or charcoal, placed in a mixture, however voluminous, of oxygen and hydrogen, makes them combine to form water; and diastase makes the starch in grains undergo transformation, and sugar is produced. And that pepsin acts in some such manner appears probable from the very minute quantity capable of exerting the peculiar digestive action on a large quantity of food, and apparently with little diminution in its active power. The process differs from ordinary fermentation, in being unattended with the formation of carbonic acid, in not requiring the presence of oxygen, and in being unaccompanied by the production of new quantities of the active principle, or ferment. It agrees with the processes of both fermentation and organic catalysis, in that whatever alters the composition of the pepsin (such as heat above 100°, strong alcohol, or strong acids), destroys the digestive power of the fluid.

Changes of the Food in the Stomach.

The general effect of digestion in the stomach is the conversion of the food into *chyme*, a substance of various composition according to the nature of the food, yet always presenting a characteristic thick, pultaceous, grumous consistence, with the undigested portions of the food mixed in a more fluid substance, and a strong, disagreeable acid odour and taste. Its colour depends on the nature of the food, or on the admixture of yellow or green bile which may, apparently, even in health, pass into the stomach.

Reduced into such a substance, all the various materials of a meal may be mingled together, and near the end of the digestive process hardly admit of recognition; but the experiments of artificial digestion, and the examination of stomachs with fistulæ, have illustrated many of the changes through which the chief alimentary principles pass, and the times and modes in which they are severally disposed of. These must now be traced.

The readiness with which the gastric fluid acts on the several articles of food is, in some measure, determined by the state of division, and the tenderness and moisture of the substance presented to it. By minute division of the food, the extent of surface with which the digestive fluid can come in contact is increased, and its action proportionably accelerated. Tender and moist substances offer less resistance to the action of the gastric juice than tough, hard, and dry ones do, because they may be thoroughly penetrated by it, and thus be attacked not only at the surface, but at every part at once. The readiness with which a substance is acted upon by the gastric fluid does not, however, necessarily imply the degree of its nutritive property; for a substance may be nutritious, yet, on account of its toughness and other qualities, hard to digest; and many soft, easily digested substances contain comparatively a small amount of nutriment. But for a

substance to be nutritive, it must be capable of being assimilated to the blood; and to find its way into the blood, it must, if insoluble, be digestible by the gastric fluid or some other secretion in the intestinal canal. There is, therefore, thus far, a necessary connection between the digestibility of a substance and its power of affording nutriment.

Those portions of food which are *liquid* when taken into the stomach, or which are easily soluble in the fluids therein, are probably at once absorbed by the blood-vessels in the mucous membrane of the stomach. Magendie's experiments, and better still, those of Dr. Beaumont, have proved this quick absorption of water, wine, weak saline solutions, and the like; that they are absorbed without manifest change by the digestive fluid, and that, generally, the water of such liquid food as soups is absorbed at once, so that the substances suspended in it are concentrated into a thicker material, like the chyme from solid food, before the digestive fluid acts upon them.

The *action of the gastric fluid* on the several kinds of *solid food* has been studied in various ways. In the earliest experiments, perforated metallic and glass tubes, filled with the alimentary substances, were introduced into the stomachs of animals, and after the lapse of a certain time withdrawn, to observe the condition of the contained substances; but such experiments are fallacious, because gastric fluid has not ready access to the food. A better method was practised in a series of experiments by Tiedemann and Gmelin, who fed dogs with different substances, and killed them in a certain number of hours afterwards. But the results they obtained are of less interest than those of the experiments of Dr. Beaumont on his patient, St. Martin, and of Dr. Gosse, who had the power of vomiting at will.

Dr. Beaumont's observations show, that the process of digestion in the stomach, during health, takes place so

rapidly, that a full meal, consisting of animal and vegetable substances, may nearly all be converted into chyme in about an hour, and the stomach left empty in two hours and a half. The details of two days' experiments will be sufficient examples:—

Exp. 42.—April 7th, 8 A.M. St. Martin breakfasted on three hard-boiled eggs, pancakes, and coffee. At half-past eight o'clock, Dr. Beaumont examined the stomach, and found a heterogeneous mixture of the several articles slightly digested. . . . . At a quarter past ten, no part of the breakfast remained in the stomach.

Exp. 43.—At eleven o'clock the same day, he ate two roasted eggs and three ripe apples. In half an hour they were in an incipient state of digestion; and a quarter past twelve no vestige of them remained.

Exp. 44.—At two o'clock P.M. the same day, he dined on roasted pig and vegetables. At three o'clock they were half chymified, and at half-past four nothing remained but a very little gastric juice.

Again, Exp. 46.—April 9th. At three o'clock P.M. he dined on boiled dried codfish, potatoes, parsnips, bread, and drawn butter. At half-past three o'clock examined, and took out a portion about half digested; the potatoes the least so. The fish was broken down into small filaments; the bread and parsnips were not to be distinguished. At four o'clock, examined another portion. Very few particles of fish remained entire. Some of the few potatoes were distinctly to be seen. At half-past four o'clock, he took out and examined another portion; all completely chymified. At five o'clock stomach empty.

Many circumstances besides the nature of the food are apt to influence the process of chymification. Among them are, the quantity of food taken; the stomach should be fairly filled, not distended: the time that has elapsed since the last meal, which should be at least enough for the stomach to be quite clear of food: the amount of exercise

previous and subsequent to the meal, gentle exercise being favourable, over-exertion injurious to digestion; the state of mind—tranquillity of temper being apparently essential to a quick and due digestion: the bodily health: the state of the weather. But under ordinary circumstances, from three to four hours may be taken as the average time occupied by the digestion of a meal in the stomach.

Dr. Beaumont constructed a table showing the times required for the digestion of all usual articles of food in St. Martin's stomach, and in his gastric fluid taken from the stomach. Among the substances most quickly digested were rice and tripe, both of which were chymified in an hour; eggs, salmon, trout, apples, and venison, were digested in an hour and a half; tapioca, barley, milk, liver, fish, in two hours; turkey, lamb, potatoes, pig, in two hours and a half; beef and mutton required from three hours to three and a half, and both were more digestible than veal; fowls were like mutton in their degree of digestibility. Animal substances were, in general, converted into chyme more rapidly than vegetables.

Dr. Beaumont's experiments were all made on ordinary articles of food. A minuter examination of the changes produced by gastric digestion on various tissues has been made by Dr. Rawitz, who examined microscopically the product of the artificial digestion of different kinds of food, and the contents of the fæces after eating the same kinds of food. The general results of his examinations, as regards *animal* food, show that muscular tissue breaks up into its constituent fasciculi, and that these again are divided transversely; gradually the transverse striæ become indistinct, and then disappear; and finally, the sarcolemma seems to be dissolved, and no trace of the tissue can be found in the chyme, except a few fragments of fibres. These changes ensue most rapidly in the flesh of fish and hares, less rapidly in that of poultry and other animals. The cells of cartilage and fibro-cartilage, except those of fish,

pass unchanged through the stomach and intestines, and may be found in the fæces. The interstitial tissues of these structures are converted into pulpy textureless substances in the artificial digestive fluid, and are not discoverable in the fæces. Elastic fibres are unchanged in the digestive fluid. Fat-cells are sometimes found quite unaltered in the fæces: and crystals of cholesterin may usually be obtained from fæces, especially after the use of pork fat.

As regards *vegetable* substances, Dr. Rawitz states, that he frequently found large quantities of cell-membranes unchanged in the fæces; also starch-cells, commonly deprived of only part of their contents. The green colouring principle, chlorophyll, was usually unchanged. The walls of the sap-vessels and spiral vessels were quite unaltered by the digestive fluid, and were usually found in large quantities in the fæces; their contents, probably, were removed.

From these experiments, we may understand the *structural* changes which the chief alimentary substances undergo in their conversion into chyme; and the proportions of each which are not reducible to chyme, nor capable of any further act of digestion. The *chemical* changes undergone in and by the proximate principles are less easily traced.

Of the *albuminous* principles, some, as the casein of milk, are coagulated by the acid of the gastric fluid; and thus, before they are digested, come into the condition of the other solid principles of the food. These, including solid albumen and fibrin, in the same proportion that they are broken up and anatomically disorganized by the gastric fluid, appear to be reduced or *lowered* in their chemical composition. This chemical change is probably produced, as suggested by Dr. Prout, by the principles entering into combination with water. It is sufficient to conceal nearly all their characteristic properties; the albumen is rendered scarcely coagulable by heat; the gelatin, even when its solution is evaporated, does not congeal in cooling; the

fibrin and casein cannot be found by their characteristic tests. It would seem, indeed, that all these various substances are converted into one and the same principle, a low form of albumen, not precipitable by nitric acid or heat, and now generally termed *albuminose* or *peptone*, from which, after being absorbed, they are again raised, in the elaboration of the blood, to which they are ultimately assimilated.

The change of molecular constitution suffered by the albuminous parts of the food, in consequence of the action of the gastric juice, has an important relation to their absorption by the blood-vessels of the stomach. From the condition of 'colloids,' or substances, so named by Professor Graham, which are absorbed with extreme difficulty, they appear, from experiments of Funke, to assume to a great degree the character of 'crystalloids,' which can pass through animal membranes with ease.*

Whatever be the mode in which the gastric secretion affects these principles, it, or something like it, appears essential, in order that they may be assimilated to the blood and tissues. For, when Bernard and Barreswil injected albumen dissolved in water into the jugular veins of dogs, they always, in about three hours after, found it in the urine. But if, previous to injection, it was mixed with gastric fluid, no trace of it could be detected in the urine. The influence of the liver seems to be almost as efficacious as that of the gastric fluid, in rendering albumen assimilable; for Bernard found that, if diluted egg-albumen, unmixed with gastric fluid, is injected into the portal vein, it no longer makes its appearance in the urine, and is, therefore, no doubt, assimilated by the blood.

Probably, most of the albuminose, with other soluble and fluid materials, is absorbed directly from the stomach by the minute blood-vessels with which the mucous membrane is so abundantly supplied.

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* These terms will be further explained and illustrated in the Chapter on Absorption.

The *saccharine* including the *amylaceous* principles are at first, probably, only mechanically separated from the vegetable substances within which they are contained, by the action of the gastric fluid. The soluble portions, viz., dextrin and sugar, are probably at once absorbed. The insoluble ones, viz., starch and lignin, (or some parts of them) are rendered soluble and capable of absorption, by being converted into dextrin or grape-sugar. It is probable that this change is carried on to some extent in the stomach; but this conversion of starch into sugar is effected, not by the gastric fluid, but by the saliva introduced with the food, or subsequently swallowed. The transformation of starch is continued in the intestinal canal, as will be shown, by the secretion of the pancreas, and perhaps by that of the intestinal glands and mucous membrane. The power of digesting uncooked starch is, however, very limited in man and Carnivora, for when starch has been taken raw, as in corn and rice, large quantities of the granules are passed unaltered with the excrements. Cooking, by expanding or bursting the envelopes of the granules, renders their interior more amenable to the action of the digestive organs; and the abundant nutriment furnished by bread, and the large proportion that is absorbed of the weight consumed, afford proof of the completeness of their power to make its starch soluble and prepare it for absorption.

Of the *oleaginous principles,*—as to their changes in the stomach, no more can be said than that they appear to be reduced to minute particles, and pass into the intestines mingled with the other constituents of the chyme. In the case of the solid fats, this effect is probably produced by the solvent action of the gastric juice on the areolar tissue, albuminous cell-walls, etc., which enter into their composition, and by the solution of which the true fat is able to mingle more uniformly with the other constituents of the chyme. Being further changed in the intestinal canal, fat is rendered capable of absorption by the lacteals.

Movements of the Stomach.

It has been already said, that the gastric fluid is assisted in accomplishing its share in digestion by the movements of the stomach. In granivorous birds, for example, the contraction of the strong muscular gizzard affords a necessary aid to digestion, by grinding and triturating the hard seeds which constitute part of the food. But in the stomachs of man and Mammalia the motions of the muscular coat are too feeble to exercise any such mechanical force on the food; neither are they needed, for mastication has already done the mechanical work of a gizzard; and the experiments of Réaumur and Spallanzani have demonstrated that substances enclosed in perforated tubes, and consequently protected from mechanical influence, are yet digested.

The normal actions of the muscular fibres of the human stomach appear to have a three-fold purpose; first, to adapt the stomach to the quantity of food in it, so that its walls may be in contact with the food on all sides, and, at the same time, may exercise a certain amount of compression upon it; secondly, to keep the orifices of the stomach closed until the food is digested; and, thirdly, to perform certain peristaltic movements, whereby the food, as it becomes chymified, is gradually propelled towards, and ultimately through, the pylorus. In accomplishing this latter end, the movements without doubt materially contribute towards effecting a thorough intermingling of the food and the gastric fluid.

When digestion is not going on, the stomach is uniformly contracted, its orifices not more firmly than the rest of its walls; but, if examined shortly after the introduction of food, it is found closely encircling its contents, and its orifices are firmly closed like sphincters. The cardiac orifice, every time food is swallowed, opens to admit its passage to the stomach, and immediately again closes. The pyloric orifice, during the first part of gastric digestion, is usually

so completely closed, that even when the stomach is separated from the intestines, none of its contents escape. But towards the termination of the digestive process, the pylorus seems to offer less resistance to the passage of substances from the stomach; first it yields to allow the successively digested portions to go through it; and then it allows the transit of even undigested substances.

From the observations of Dr. Beaumont on the man St. Martin, it appears that food, so soon as it enters the stomach, is subjected to a kind of peristaltic action of the muscular coat, whereby the digested portions are gradually approximated towards the pylorus. The movements were observed to increase in rapidity as the process of chymification advanced, and were continued until it was completed.

The contraction of the fibres situated towards the pyloric end of the stomach seems to be more energetic and more decidedly peristaltic than those of the cardiac portion. Thus, Dr. Beaumont found that when the bulb of the thermometer was placed about three inches from the pylorus, it was tightly embraced from time to time and drawn towards the pyloric orifice for a distance of three or four inches. The object of this movement appears to be, as just said, to carry the food towards the pylorus as fast as it is formed into chyme, and to propel the chyme into the duodenum; the undigested portions of food being kept back until they are also reduced into chyme, or until all that is digestible has passed out. The action of these fibres is often seen in the contracted state of the pyloric portion of the stomach after death, when it alone is contracted and firm, while the cardiac portion forms a dilated sac. Sometimes, by a predominant action of strong circular fibres placed between the cardia and pylorus, the two portions, or ends as they are called, of the stomach, are separated from each other by a kind of hour-glass contraction.

The interesting researches of Dr. Brinton have clearly established that, by means of this peristaltic action of the

muscular coats of the stomach, not merely is chymified food gradually propelled through the pylorus, but a kind of double current is continually kept up among the contents of the stomach, the circumferential parts of the mass being gradually moved onward towards the pylorus by the peristaltic contraction of the muscular fibres, while the central portions are propelled in the opposite direction, namely, towards the cardiac orifice; in this way is kept up a constant circulation of the contents of the viscus, highly conducive to their free mixture with the gastric fluid and to their ready digestion.

These actions of the stomach are peculiar to it and independent. But it is, also, adapted to act in concert with the abdominal muscles, in certain circumstances which can hardly be called abnormal, as in vomiting and eructation. It has indeed been frequently stated that the stomach itself is quite passive during vomiting, and that the expulsion of its contents is effected solely by the pressure exerted upon it when the capacity of the abdomen is diminished by the contraction of the diaphragm, and subsequently of the abdominal muscles. The experiments and observations, however, which are supposed to confirm this statement, only show that the contraction of the abdominal muscles alone is sufficient to expel matters from an unresisting bag through the œsophagus; and that, under very abnormal circumstances, the stomach, by itself, cannot or rather does not expel its contents. They by no means show that in ordinary vomiting the stomach is passive; and, on the other hand, there are good reasons for believing the contrary.

It is true that facts are wanting to demonstate with certainty this action of the stomach in vomiting; but some of the cases of fistulous opening into the organ appear to support the belief that it does take place;* and the

* A collection of cases of fistulous communication with the stomach, through the abdominal parietes, has been given by Dr. Murchison in vol. xli. of the Medico-Chirurgical Transactions.

analogy of the case of the stomach with that of the other hollow viscera, as the rectum and bladder, may be also cited in confirmation.

Besides the influence which it may thus have by its contraction, the stomach also essentially contributes to the act of vomiting, by the contraction of its pyloric orifice at the same time that the oblique fibres around the cardiac orifice are relaxed. For, until the relaxation of these fibres, no vomiting can ensue; when contracted, they can as well resist all the force of the contracting abdominal and other muscles, as the muscles by which the glottis is closed can resist the same force in the act of straining. Doubtless we may refer many of the acts of retching and ineffectual attempts to vomit, to the want of concord between the relaxation of these muscles and the contraction of the others.

The muscles with which the stomach co-operates in contraction during vomiting, are chiefly and primarily those of the abdomen; the diaphragm also acts, but not as the muscles of the abdominal walls do. They contract and compress the stomach more and more towards the back and upper parts of the diaphragm; and the diaphragm (which is usually drawn down in the deep inspiration that precedes each act of vomiting) holds itself fixed in contraction, and presents an unyielding surface against which the stomach may be pressed. It is enabled to act thus, and probably only thus, because the inspiration which precedes the act of vomiting is terminated by the closure of the glottis; after which the diaphragm can neither descend further, except by expanding the air in the lungs, nor, except by compressing the air, ascend again until, the act of vomiting having ceased, the glottis is opened again (see diagram, p. 231; see also p. 233).

Some persons possess the power of vomiting at will, without applying any undue irritation to the stomach, but simply by a voluntary effort. It seems also, that this power may be acquired by those who do not naturally pos-

sess it, and by continual practice may become a habit. There are cases also of rare occurrence in which persons habitually swallow their food hastily, and nearly unmasticated, and then at their leisure regurgitate it, piece by piece, into their mouth, remasticate, and again swallow it, exactly as is done by the ruminant order of Mammalia.

Influence of the Nervous System on Gastric Digestion.

This influence is manifold; and is evidenced, 1*st*, in the sensations which induce to the taking of food; 2*nd*, in the secretion of the gastric fluid; 3*rd*, in the movements of the food in and from the stomach.

The sensation of *hunger* is manifested in consequence of deficiency of food in the system. The mind refers the sensation to the stomach; yet since the sensation is relieved by the introduction of food either into the stomach itself, or into the blood through other channels than the stomach, it would appear not to depend on the state of the stomach alone. This view is confirmed by the fact, that the division of both pneumogastric nerves, which are the principal channels by which the mind is cognisant of the condition of the stomach, does not appear to allay the sensations of hunger.

But that the stomach has some share in this sensation is proved by the relief afforded, though only temporarily, by the introduction of even non-alimentary substances into this organ. It may, therefore, be said that the sensation of hunger is derived from the system generally, but chiefly from the condition of the stomach, the nerves of which, we may suppose, are more affected by the state of the insufficiently replenished blood than those of other organs are.

The sensation of *thirst*, indicating the want of fluid, is referred to the fauces, although, as in hunger, this is merely the local declaration of a general condition existing in the system. For thirst is relieved for only a very short

time by moistening the dry fauces; but may be relieved completely by the introduction of liquids into the blood, either through the stomach, or by injections into the blood-vessels, or by absorption from the surface of the skin or the intestines. The sensation of thirst is perceived most naturally whenever there is a disproportionately small quantity of water in the blood: as well, therefore, when water has been abstracted from the blood, as when saline or any solid matters have been abundantly added to it. We can express the fact (even if it be not an explanation of it), by saying that the nerves of the mouth and fauces, through which the sense of thirst is chiefly derived, are more sensitive to this condition of the blood than other nerves are. And the cases of hunger and thirst are not the only ones in which the mind derives, from certain orgaus, a peculiar predominant sensation of some condition affecting the whole body. Thus, the sensation of the "necessity of breathing," is referred especially to the lungs; but, as Volkmann's experiments show, it depends on the condition of the blood which circulates everywhere, and is felt even after the lungs of animals are removed; for they continue, even then, to gasp and manifest the sensation of want of breath. And, as with respiration when the lungs are removed, the mind may still feel the body's want of breath; so in hunger and thirst, even when the stomach has been filled with innutritious substances, or the pneumogastric nerves have been divided, and the mouth and fauces are kept moist, the mind is still aware, by the more obscure sensations in other parts, of the whole body's need of food and water.

The *influence of the nervous system on the secretion of gastric fluid*, is shown plainly enough in the influence of the mind upon digestion in the stomach; and is, in this regard, well illustrated by several of Dr. Beaumont's observations. M. Bernard also, watching the act of gastric digestion in

dogs which had fistulous openings into their stomachs, saw that on the instant of dividing their pneumogastric nerves, the process of digestion was stopped, and the mucous membrane of the stomach, previously turgid with blood, became pale, and ceased to secrete. These, however, and the like experiments showing the instant effect of division of the pneumogastric nerves, may prove no more than the effect of a severe shock, and the fact that influences affecting digestion may be conveyed to the stomach through those nerves. From other experiments it may be gathered, that although, as in M. Bernard's, the division of both pneumogastric nerves always temporarily suspends the secretion of gastric fluid, and so arrests the process of digestion, and is occasionally followed by death from inanition; yet the digestive powers of the stomach may be completely restored after the operation, and the formation of chyme and the nutrition of the animal may be carried on almost as perfectly as in health.

In thirty experiments on Mammalia, which M. Wernscheidt performed under Müller's direction, not the least difference could be perceived in the action of narcotic poisons introduced into the stomach, whether the pneumogastric had been divided on both sides or not, provided the animals were of the same species and size. It appears, however, that such poisons as are capable of being rendered inert by the action of the gastric fluid, may, if taken into the stomach shortly after division of both pneumogastric nerves, produce their poisonous effects; in consequence, apparently, of the temporary suspension of the secretion of gastric fluid. Thus, in one of his experiments, M. Bernard gave to each of two dogs, in one of which he had divided the pneumogastric nerves, a dose of emulsine, and half an hour afterwards a dose of amygdaline, substances which are innocent alone, but when mixed produce hydrocyanic acid. The dog whose nerves were cut, died in a quarter of an hour, the sub-

stances being absorbed unaltered and mixing in the blood; in the other, the emulsine was decomposed by the gastric fluid before the amygdaline was administered; therefore, hydrocyanic acid was not formed in the blood, and the dog survived.

The influence of the pneumogastric nerves over the secretion of gastric fluid has been of late even more decidedly shown by M. Bernard, who found that galvanic stimulus of these nerves excited an active secretion of the fluid, while a like stimulus applied to the sympathetic nerves issuing from the semilunar ganglia, caused a diminution and even complete arrest of the secretion.

The influence of the nervous system on the movements of the stomach has been often seen in the retardation or arrest of these movements after division of the pneumogastric nerves. The results of irritating the same nerves were ambiguous; but the experiments of Longet and Bischoff have shown that the different results depended on whether the stomach were digesting or not at the time of the experiment. In the act of digestion, the nervous system of the stomach appears to participate in the excitement which prevails through the rest of its organization, and a stimulus applied to the pneumogastric nerves is felt intensely, and active movements of the muscular fibres of the stomach follow; but in the inaction of fasting, the same stimulus produces no effect. So, while the stomach is digesting, the pylorus is too irritable to allow anything but chyme to pass; but when digestion is ended, the undigested parts of the food, and even large bodies, coins, and the like, may pass through it.

Digestion of the Stomach after Death.

If an animal die during the process of gastric digestion, and when, therefore, a quantity of gastric juice is present in the interior of the stomach, the walls of this organ itself

are frequently themselves acted on by their own secretion, and to such an extent, that a perforation of considerable size may be produced, and the contents of the stomach may in part escape into the cavity of the abdomen. This phenomenon is not unfrequently observed in *post-mortem* examinations of the human body; but, as Dr. Pavy observes, the effect may be rendered, by experiment, more strikingly manifest. "If, for instance," he remarks, "an animal, as a rabbit, be killed at a period of digestion, and afterwards exposed to artificial warmth to prevent its temperature from falling, not only the stomach, but many of the surrounding parts will be found to have been dissolved. With a rabbit killed in the evening, and placed in a warm situation (100° to 110° Fahr.) during the night, I have seen in the morning, the stomach, diaphragm, part of the liver and lungs, and the intercostal muscles of the side upon which the animal was laid all digested away, with the muscles and skin of the neck and upper extremity on the same side also in a semi-digested state."

From these facts, it becomes an interesting question why, during life, the stomach is free from liability to injury from a secretion, which, after death, is capable of such destructive effects? John Hunter, who particularly drew attention to the phenomena of *post-mortem* digestion, explained the immunity from injury of the living stomach, by referring it to the protective influence of the "vital principle." But this dictum has been called in question by subsequent observers. It is, indeed, rather a statement of a fact, than an explanation of its cause. It must be confessed, however, that no entirely satisfactory theory has been yet stated as a substitute.

It is only necessary to refer to the idea of Bernard, that the living stomach finds protection from its secretion in the presence of epithelium and mucus, which are constantly renewed in the same degree that they are constantly dis-

solved, in order to remark that this theory has been disproved by experiments of Pavy's, in which the mucous membrane of the stomachs of dogs was dissected off for a small space, and, on killing the animals some days afterwards, no sign of digestion of the stomach was visible. "Upon one occasion, after removing the mucous membrane and exposing the muscular fibres over a space of about an inch and a half in diameter, the animal was allowed to live for ten days. It ate food every day, and seemed scarcely affected by the operation. Life was destroyed whilst digestion was being carried on, and the lesion in the stomach was found very nearly repaired: new matter had been deposited in the place of what had been removed, and the denuded spot had contracted to much less than its original dimensions."

Dr. Pavy believes that the natural alkalinity of the blood, which circulates so freely during life in the walls of the stomach, is sufficient to neutralize the acidity of the gastric juice, were it, so to speak, to make an attempt at digesting parts with which it has no business; and as may be gathered from what has been previously said (p. 283), the neutralization of the acidity of the gastric secretion is quite sufficient to destroy its digestive powers. He also very ingeniously argues that this very alkalinity must, from the conditions of the circulation naturally existing in the walls of the stomach, be increased in proportion to the need of its protective influence. "In the arrangement of the vascular supply," he remarks, "a doubly effective barrier is, as it were, provided. The vessels pass from below upwards towards the surface: capillaries having this direction ramify between the tubules by which the acid of the gastric juice is secreted; and being separated by secretion below, must leave the blood that is proceeding upwards correspondingly increased in alkalinity; and thus, at the period when the largest amount of acid is flowing into the stomach, and the greatest protection is required,

then is the provision afforded in its highest state of efficiency."

Dr. Pavy's theory is the best and most ingenious hitherto framed in connection with this subject; but the experiments adduced in its favour are open to many objections, and afford only a negative support to the conclusions they are intended to prove. The matter, therefore, can scarcely be considered finally settled.

DIGESTION IN THE INTESTINES.

The intestinal canal is divided into two chief portions, named, from their differences in diameter, the *small* and *large* intestine. These are continuous with each other, and communicate by means of an opening guarded by a valve, the *ileo-cæcal* valve, which allows the passage of the products of digestion from the small into the large bowel, but not, under ordinary circumstances, in the opposite direction.

The structure and functions of each organ or tissue concerned in intestinal digestion will be first described in detail, and afterwards a summary will be given of the changes which the food undergoes in its passage through the intestines, 1st, from the pylorus to the ileo-cæcal valve; and, 2nd, from the ileo-cæcal valve to the anus.

Structure and Secretions of the Small Intestine.

The small intestine, the average length of which in an adult is about twenty feet, has been divided, for convenience of description, into three portions, viz., the *duodenum*, which extends for eight or ten inches beyond the pylorus; the *jejunum*, which occupies two-fifths, and the *ileum*, which occupies three-fifths of the rest of the canal.

The small intestine, like the stomach, is constructed of three principal coats, viz., the serous, muscular, and mucous. The *serous* coat, formed by the visceral layer of the peritoneum, need not be here specially described. The fibres of the *muscular* coat of the small intestine are arranged in two layers; those of the outer layer being

disposed longitudinally; those of the inner layer transversely, or in portions of circles encompassing the canal. They are composed of the unstriped kind of muscular fibre.

Between the mucous and muscular coats, there is a layer of submucous tissue, in which numerous blood-vessels and a rich plexus of nerves and ganglia are imbedded (Meissner).

The *mucous membrane* is the most important coat in relation to the function of digestion. The following structures which enter into its composition of the mucous membrane may be now successively described;—the *valvulæ conniventes;* the *villi;* and the *glands.* The general structure of the mucous membrane of the intestines resembles that of the stomach (p. 266), and, like it, is lined on its inner surface by columnar epithelium. *Lymphoid* or *Retiform* tissue (fig. 72) enters largely into its construction; and on its deep surface is a layer of the *muscularis mucosæ* (p. 276).

*Fig. 72.**

Valvulæ Conniventes.

The valvulæ conniventes commence in the duodenum, about one or two inches beyond the pylorus, and becoming larger and more numerous immediately beyond the entrance of the bile-duct, continue thickly arranged and well developed throughout the jejunum; then, gradually diminishing in size and number, they cease near the

* Fig. 72. The figure represents a cross section of a small fragment of the mucous membrane, including one entire crypt of Lieberkühn and parts of several others: *a*, cavity of the tubular glands or crypts; *b*, one of the lining epithelial cells; *c*, the lymphoid or retiform spaces, of which some are empty, and others occupied by lymph cells, as at *d*.

middle of the ileum. In structure they are formed by a doubling inwards of the mucous membrane, the crescentic, nearly circular, folds thus formed being arranged transversely with regard to the axis of the intestine, and each individual fold seldom extending around more than ½ or ⅔ of the bowel's circumference. Unlike the rugæ in the stomach, they do not disappear on distension. Only an imperfect notion of their natural position and function can be obtained by looking at them after the intestine has been laid open in the usual manner. To understand them aright, a piece of gut should be distended either with air or alcohol, and not opened until the tissues have become hardened. On then making a section, it may be seen that instead of disappearing, as the rugæ in the stomach would under similar circumstances, they stand out at right angles to the general surface of the mucous membrane (fig. 73). Their functions are probably these—Besides (1) offering a largely increased surface for secretion and absorption, they probably (2) prevent the too rapid passage of the very liquid products of gastric digestion, immediately after their escape from the stomach, and (3), by their projection, and consequent interference with an uniform and untroubled current of the intestinal contents, probably assist in the more perfect mingling of the latter with the secretions poured out to act on them.

Fig. 73.*

Glands of the Small Intestine.—The glands are of three principal kinds, named after their describers, the glands of Lieberkühn, of Peyer, and of Brunn. The *glands* or *fol-*

* Fig. 72. Piece of small intestine (previously distended and hardened by alcohol) laid open to show the normal position of the valvulæ conniventes.

licles of Lieberkühn are simple tubular depressions of the intestinal mucous membrane, thickly distributed over the whole surface both of the large and small intestines. In the small intestine they are visible only with the aid of a lens; and their orifices appear as minute dots scattered between the villi. They are larger in the large intestine, and increase in size the nearer they approach the anal end of the intestinal tube; and in the rectum their orifices may be visible to the naked eye. In length they vary from $\frac{1}{30}$ to $\frac{1}{10}$ of a line. Each tubule (fig. 74) is constructed of the same essential parts as the intestinal mucous membrane, viz., a fine structureless *membrana propria*, or basement membrane, a layer of cylindrical epithelium lining it and capillary blood-vessels covering its exterior. Their contents appear to vary, even in health; the varieties being dependent, probably, on the period of time in relation to digestion at which they are examined. At the bottom of the follicle, the contents usually consist of a granular material, in which a few cytoblasts or nuclei are imbedded; these cytoblasts, as they ascend towards the surface, are supposed to be gradually developed into nucleated cells, some of which are discharged into the intestinal cavity. The purpose served by the material secreted by these glands is still doubtful. Their large number and the extent of surface occupied by them, seem, however, to indicate that they are concerned in other and higher offices than the mere production of fluid to moisten the surface of the mucous membrane, although, doubtless, this is one of their functions.

Fig. 74.*

The *glands of Peyer* occur exclusively in the small intestine. They are found in greatest abundance in the lower part of the ileum near to the ileo-cæcal valve. They are

* Fig. 74. A gland of Lieberkühn.

met with in two conditions, viz., either scattered singly, in which case they are termed *glandulæ solitariæ*, or aggregated in groups varying from one to three inches in length and about half-an-inch in width, chiefly of an oval form, their long axis parallel with that of the intestine. In this state, they are named *glandulæ agminatæ*, the groups being commonly called *Peyer's patches* (fig. 75). The latter are placed almost always opposite the attachment of the mesentery. In structure, and probably in function, there is no essential difference between the solitary glands and

Fig. 56.

Fig 56

soon as possible

the individual bodies of which each group or patch is made up; but the surface of the solitary glands (fig. 76) is beset with villi, from which those forming the agminate patches (fig. 77) are usually free. In the condition in which they have been most commonly examined, each gland appears as a circular opaque-white sacculus, from half a line to a line in diameter, and, according to the degree in which it is developed, either sunk beneath, or more or less prominently raised on, the surface of a depression or fossa in the mucous membrane. Each gland

* Fig. 75. Agminate follicles, or *Peyer's patch*, in a state of distension: magnified about 5 diameters (after Boehm).

Leave out the dark border

is surrounded by openings like those of Lieberkühn's follicles (see fig. 77) except that they are more elongated; and the direction of the long diameter of each opening is such that the whole produce a radiated appearance around the white sacculus. These openings appear to belong to tubules identical with Lieberkühn's follicles: they have no communication with the sacculus, and none of its contents escape through them on pressure. Neither can any

Not there

Fig. 76.*

Fig. 77.†

permanent opening be detected in the sacculus or Peyer's gland itself (see fig. 78).

Each gland is an imperfectly closed sac or follicle formed of a tolerably firm membranous capsule of fine connective tissue, imbedded in a rich plexus of minute blood-vessels, many fine branches from which pass through the capsule and enter, chiefly loopwise, the interior of the follicle (fig. 79). Entering into the formation of the sacculus,

* Fig. 76. Solitary gland of small intestine, after Boehm.

† Fig. 77. Part of a patch of the so-called Peyer's glands magnified, showing the various forms of the sacculi, with their zone of foramina. The rest of the membrane marked with Lieberkühn's follicles, and *sprinkled* with villi (after Boehm).

moreover, and forming a *stroma* or supporting framework throughout its interior, is *lymphoid* or *adenoid* tissue (fig. 72), continuous with that which forms a great part of the mucous membrane outside it. The contents of each sac consist of a pale greyish opalescent pulp, formed of albuminous and fatty matter, and a multitude of nucleated corpuscles of various sizes, resembling exactly those found in lymphatic glands.

The real office of these Peyerian glands or follicles is still unknown. It was formerly believed that each follicle was a kind of secreting cell, which, when its contents were fully matured, formed a communication with the cavity of the intestine by the absorption or bursting of its own cell-wall, and of the portion of mucous membrane over it, and thus discharged its secretion into the intestinal canal. A small shallow cavity or space was thought to remain, for a time, after this absorption or dehiscence, but shortly to disappear, together with all trace of the previous gland.

Fig. 78*.

More recent acquaintance with the real structure of these bodies seems, however, to prove that they are not mere temporary gland-cells which thus discharge their elaborated contents into the intestine and then disappear, but that they are rather to be regarded as structures

* Fig. 78. Side-view of a portion of intestinal mucous membrane of a cat, showing a Peyer's gland (*a*): it is imbedded in the submucous tissue (*f*), the line of separation between which and the mucous membrane passes across the gland : *b*, one of the tubular follicles, the orifices of which form the zone of openings around the gland : *c*, the fossa in the mucous membrane : *d*, villi : *e*, follicles of Lieberkühn (after Bendz).

analogous to lymphatic or absorbent glands, and that their office is to take up certain materials from the chyle, elaborate and subsequently discharge them into the lacteals, with which vessels they appear to be closely connected, although no direct communication has been proved to exist between them.

Moreover, it has been lately suggested that since the molecular and cellular contents of the glands are so abundantly traversed by minute blood-vessels, important

Fig. 79*.

changes may mutually take place between these contents and the blood in the vessels, material being abstracted from the latter, elaborated by the cells, and then restored

* Fig. 79. Transverse section of injected Peyer's glands (from Kölliker. The drawing was taken from a preparation made by Frey: it represents the fine capillary looped network spreading from the surrounding blood-vessels into the interior of three of Peyer's capsules from the intestine of the rabbit.

to the blood, much in the same manner as is believed to be the case in the so-called vascular glands, such as the spleen, thymus, and others; and that thus Peyer's glands should also be regarded as closely analogous to these vascular glands. Possibly they may combine the functions both of lymphatic and vascular glands, absorbing and elaborating material both from the chyle and from the blood within their minute vessels, and transmitting part of the lacteal system and part direct to the blood.

Fig. 80.*

Brunn's glands (fig. 80) are confined to the duodenum; they are most abundant and thickly set at the commencement of this portion of the intestine, diminishing gradually as the duodenum advances. Situated beneath the mucous membrane, and imbedded in the submucous tissue, they are minutely lobulated bodies, visible to the naked eye, like detached small portions of pancreas, and provided with permanent gland-ducts, which pass through the mucous membrane and open on the internal surface of the intestine.

* Fig. 80. Enlarged view of one of Brunn's glands from the human duodenum (from Frey). The main duct is seen superiorly; its branches are elsewhere hidden by the bunches of opaque glandular vesicles.

As in structure, so probably in function, they resemble the pancreas; or at least stand to it in a similar relation to that which the small labial and buccal glands occupy in relation to the larger salivary glands, the parotid and submaxillary.

The *Villi* (figs. 81, 82) are confined exclusively to the mucous membrane of the *small* intestine. They are minute vascular processes, from a quarter of a line to a line and two-thirds in length, covering the surface of the mucous membrane, and giving it a peculiar velvety, fleecy appearance. Krauss estimates them at fifty to ninety in number in a square line, at the upper part of the small intestine, and at forty to seventy in the same area at the lower part. They vary in form even in the same animal, and differ according as the lymphatic vessels they contain are empty or full of chyle; being usually, in the former case, flat and pointed at their summits, in the latter cylindrical or clavate.

Each villus consists of a small projection of mucous membrane, and its interior is therefore supported throughout by fine retiform or adenoid tissue, which forms the framework or stroma in which the other constituents are contained.

The surface of the villus is clothed by columnar epithelium, which rests on a fine basement membrane; while within this are found, reckoning from without inwards, blood-vessels, fibres of the *muscularis mucosæ*, and a single lymphatic or lacteal vessel rarely looped or branched (fig. 81); besides granular matter, fat-globules, etc.

The *epithelium* is of the columnar kind, and continuous with that lining the other parts of the mucous membrane. The cells are arranged with their long axis radiating from the surface of the villus (fig. 81), and their smaller ends resting on the basement membrane. Some doubt exists concerning the minute structure of these cells and their relation to the deeper parts of the villus.

Beneath the basement or limiting membrane there is a rich supply of *blood-vessels*. Two or more minute arteries are distributed within each villus; and from their capil-

Fig. 81.*

laries, which form a dense network, proceed one or two small veins, which pass out at the base of the villus.

The layer of the *muscularis mucosæ* in the villus forms a kind of thin hollow cone immediately around the central lacteal, and is, therefore, situate beneath the blood-vessels. The addition of acetic acid to the villus brings out the characteristic nuclei of the muscular fibres, and shows the size and position of the layer most distinctly. Its use is

* Fig. 81. (Slightly altered from Teichmann.) A. Villus of sheep. B. Villi of man.

still unknown, although it is impossible to resist the belief, that it is instrumental in the propulsion of chyle along the lacteal.

Fig. 82.*

The *lacteal vessel* enters the base of each villus, and pass-

* Fig. 82. (From Teichmann.) A, lacteals in villi. P, Peyer's glands. B and D, superficial and deep network of lacteals in submucous tissue. L, Lieberkühn's glands. E, small branch of lacteal vessel on its way to mesenteric gland. H and O, muscular fibres of intestine. S, peritoneum.

ing up in the middle of it, extends nearly to the tip, where it ends commonly by a closed and somewhat dilated extremity. In the larger villi there may be two small lacteal vessels which end by a loop (fig. 81), or the lacteals may form a kind of network in the villus. The last method of ending, however, is rarely or never seen in the human subject, although common in some of the lower animals (A, fig. 81).

The office of the villi is the absorption of chyle from the completely digested food in the intestine. The mode in which they effect this will be considered in the chapter on ABSORPTION.

Structure of the Large Intestine.

The large intestine, which in an adult is from about 4 to 6 feet long, is subdivided for descriptive purposes into three portions, viz.:—The *cæcum*, a short wide pouch, communicating with the lower end of the small intestine through an opening, guarded by the *ileo-cæcal* valve; the *colon*, continuous with the cæcum, which forms the principal part of the large intestine, and is divided into an ascending, transverse and descending portion; and the *rectum*, which, after dilating at its lower part, again contracts, and immediately afterwards opens externally through the *anus*. Attached to the cæcum is the small *appendix vermiformis*.

Like the *small* intestine, the *large* is constructed of three principal coats, viz., the serous, muscular, and mucous. The *serous* coat need not be here particularly described. Connected with it are the small processes of peritoneum containing fat, called *appendices epiploicæ*. The fibres of the *muscular* coat, like those of the small intestine, are arranged in two layers—the outer longitudinally, the inner circularly. In the cæcum and colon, the longitudinal fibres, besides being, as in the small intestine, thinly disposed in all parts of the wall of the bowel, are

collected, for the most part, into three strong bands, which being shorter, from end to end, than the other coats of the intestine, hold the canal in folds, bounding intermediate sacculi. On the division of these bands, the intestine can be drawn out to its full length, and it then assumes, of course, an uniformly cylindrical form. In the rectum, the fasciculi of these longitudinal bands spread out and mingle with the other longitudinal fibres, forming with them a thicker layer of fibres than exists on any other part of the intestinal canal. The circular muscular fibres are spread over the whole surface of the bowel, but are somewhat more marked in the intervals between the sacculi. Towards the lower end of the rectum they become more numerous, and at the anus they form a strong band called the *internal sphincter* muscle.

The *mucous membrane* of the large, like that of the small intestine, is lined throughout by columnar epithelium, but, unlike it, is quite smooth and destitute of villi, and is not projected in the form of valvulæ conniventes. Its general microscopic structure resembles that of the small intestine.

Glands of the Large Intestine.—The glands with which the large intestine is provided are of two kinds, the *tubular* and *lenticular*.

The *tubular* glands, or glands of Lieberkühn, resemble those of the small intestine, but are somewhat larger and more numerous. They are also more uniformly distributed.

The *lenticular* glands are most numerous in the cæcum and vermiform appendix. They resemble in shape and structure, almost exactly, the solitary glands of the small intestine, and, like them, have no opening. Just over them, however, there is commonly a small depression in the mucous membrane, which has led to the erroneous belief that some of them open on the surface.

The functions discharged by the glands found in the

large intestine are not known with any certainty, but there is no reason to doubt that they resemble very nearly those discharged by the glands of like structure in the small intestine.

The difficulty of determining the function of any single set of the intestinal glands seems indeed almost insuperable, so many fluids being discharged together into the intestine; for all acting, probably, at once, produce a combined effect upon the food, so that it is almost impossible to discern the share of any one of them in digestion.

Ilio-cæcal valve.—The ilio-cæcal valve is situate at the place of junction of the small with the large intestine, and guards against any reflux of the contents of the latter into the ileum. It is composed of two semilunar folds of mucous membrane. Each fold is formed by a doubling inwards of the mucous membrane, and is strengthened on the outside by some of the circular muscular fibres of the intestine, which are contained between the outer surfaces of the two layers of which each fold is composed. The inner surface of the folds is smooth; the mucous membrane of the ilium being continuous with that of the cæcum. That surface of each fold which looks towards the small intestine is covered with villi, while that which looks to the cæcum has none. When the cæcum is distended, the margins of the folds are stretched, and thus are brought into firm apposition one with the other.

While the circular muscular fibres of the bowel at the junction of the ilium with the cæcum are contained between the outer opposed surfaces of the folds of mucous membrane which form the valve, the longitudinal muscular fibres and the peritoneum of the small and large intestine respectively are continuous with each other, without dipping in to follow the circular fibres and the mucous membrane. In this manner, therefore, the folding inwards of these two last named structures is preserved, while on the other hand, by dividing the longitudinal

muscular fibres and the peritoneum, the valve can be made to disappear, just as the constrictions between the sacculi of the large intestine can be made to disappear by performing a similar operation.

The Pancreas, and its Secretion.

The pancreas is situated within the curve formed by the duodenum; and its main duct opens into that part of the intestine, either through a small opening or through a duct common to itself and to the liver. The pancreas, in its minute anatomy, closely resembles the salivary glands; and the fluid elaborated by it appears almost identical with saliva. When obtained pure, in all the different animals in which it has been hitherto examined, it has been found colourless, transparent, and slightly viscid. It is alkaline when fresh, and contains a peculiar animal matter named *pancreatin* and certain salts, both of which are very similar to those found in saliva. In pancreatic secretion, however, there is no sulpho-cyanogen. Pancreatin is a substance coagulable by heat, and in many other respects very like albumen: to it the peculiar digestive power of the pancreatic secretion is probably due. Like saliva, the pancreatic fluid, shortly after its escape, becomes neutral and then acid.

The following is the mean of three analyses by Schmidt:—

Composition of Pancreatic Secretion.

Water	980·45
Solids	19·55
Pancreatin	12·71
Inorganic bases and salts	6·84
	19·55

The functions of the pancreas are probably as follows:—

1. Numerous experiments have shown, that *starch* is

acted upon by the pancreatic secretion, or by portions of pancreas put in starch-paste, in the same manner that it is by saliva and portions of the salivary glands. And although, as before stated (p. 262), many substances besides those glands can excite the transformation of starch into dextrin and grape-sugar, yet it appears probable that the pancreatic fluid, exercising this power of transformation, is largely subservient to the purpose of digesting starch. MM. Bouchardat and Sandras have shown that the raw starch-granules which have passed unchanged through the crops and gizzards of granivorous birds, or through the stomachs of herbivorous Mammalia, are, in the small intestine, disorganized, eroded, and finally dissolved, as they are when exposed, in experiment, to the action of the pancreatic fluid. The bile cannot effect such a change in starch; and it is most probable that the pancreatic secretion is the principal agent in the transformation, though it is by no means clear that the office may not be shared by the secretion of the intestinal mucous membrane, which also seems to possess the power of converting starch into sugar.

2. The existence of a pancreas in Carnivora, which have little or no starch in their food, and the results of various observations and experiments, leave very little doubt that the pancreatic secretion also assists largely in the digestion of *fatty matters*, by transforming them into a kind of emulsion, and thus rendering them capable of absorption by the lacteals. Several cases have been recorded in which the pancreatic duct being obstructed, so that the secretion could not be discharged, fatty or oily matter was abundantly discharged from the intestines. In nearly all these cases, indeed, the liver was coincidently diseased, and the change or absence of the bile might appear to contribute to the result; yet the frequency of extensive disease of the liver, unaccompanied by fatty discharges from the intestines, favours the view that, in these cases, it is to the absence of the pancreatic fluid from the intestines that the

excretion or non-absorption of fatty matter should be ascribed. In Bernard's experiments too, fat always appeared in the evacuations when the pancreas was destroyed or its duct tied. Bernard, indeed, is of opinion that to emulsify fat is the express office of the pancreas, and the evidence that he and others have brought forward in support of this view is very weighty. The power of emulsifying fat, however, although perhaps mainly exercised by the secretion of the pancreas, is evidently possessed to some extent by other secretions poured into the intestines, and especially by the bile.

3. The pancreatic secretion discharges a third function also, namely, that of dissolving albuminous substances; the peptone produced by the action of the pancreatic secretion on proteids not differing essentially from that formed by the action of the gastric juice (see p. 285).

Structure of the Liver.

The liver is an extremely vascular organ, and receives its supply of blood from two distinct vessels, the *portal vein* and *hepatic artery*, while the blood is returned from it into the vena cava inferior by the *hepatic vein*. Its secretion, the *bile*, is conveyed from it by the *hepatic duct*, either directly into the intestine, or, when digestion is not going on, into the *cystic* duct, and thence into the gall-bladder, where it accumulates until required. The portal vein, hepatic artery, and hepatic duct branch together throughout the liver, while the hepatic vein and its tributaries run by themselves.

On the outside the liver has an incomplete covering of peritoneum, and beneath this is a very fine coat of areolar tissue, continuous over the whole surface of the organ. It is thickest where the peritoneum is absent, and is continuous on the general surface of the liver with the fine, and, in the human subject, almost imperceptible, areolar tissue investing the lobules. At the transverse fissure it is

merged in the areolar investment called Glisson's capsule,

Fig. 83.*

which, surrounding the portal vein, hepatic artery, and hepatic duct, as they enter at this part, accompanies them in their branchings through the substance of the liver.

Fig. 84.

The liver is made up of small roundish or oval portions called lobules, each of which is about $\frac{1}{20}$ of an inch in diameter, and composed of the minutes branches of the portal vein, hepatic artery, hepatic duct, and hepatic vein; while the interstices of

* Fig. 83. The liver has been turned over from left to right so as expose the lower surface. 1, left lobe; 2, 3, 4, 5, right lobe; 6, lobulus quadratus; 7, pons hepatis; 8, 9, 10, lobulus Spigelii; 11, lobulus caudatus; 12, 13, transverse or portal fissure with the great vessels; 14, hepatic artery; 15, vena portæ; 16, anterior part of the longitudinal fissure, containing 17, the round ligament or obliterated remains of the umbilical vein; 18, posterior part of the same fissure, containing 19, the obliterated ductus venosus; 20, 21, 22, gall-bladder; 23, cystic duct; 24, hepatic duct; 25, fossa containing

these vessels are filled by the liver cells. These cells (fig. 84) which make up a great portion of the substance of the organ, are rounded or polygonal from about $\frac{1}{800}$ to $\frac{1}{1000}$ of an inch in diameter, containing well-marked nuclei and granules, and having sometimes a yellowish tinge, especially about their nuclei; frequently, they contain also various sized particles of fat (fig. 84 B). Each lobule is very sparingly invested by areolar tissue.

Fig. 85.*

To understand the distribution of the blood-vessels in the liver, it will be well to trace, first, the two blood-vessels and the duct which enter the organ on the under surface at the transverse fissure, viz., the portal vein, hepatic artery, and hepatic duct. As before remarked, all three run in company, and their appearance on longitudinal section is shown in fig. 85. Running together through the substance of the liver, they are contained in small channels, called *portal canals,* their immediate investment being a sheath of areolar tissue, called Glisson's capsule.

26, the vena cava inferior; 27, opening of the capsular vein; 28, small part of the trunk of the right hepatic vein; 29, trunk of the left hepatic vein; 30, 31, openings of the right and left diaphragmatic veins.

* Fig. 85. Longitudinal section of a portal canal, containing a portal vein, hepatic artery and hepatic duct, from the pig (after Kiernan). ⅚. P, branch of vena portæ, situated in a portal canal, formed amongst the lobules of the liver, and giving off vaginal branches; there are also seen within the large portal vein numerous orifices of the smallest interlobular veins arising directly from it; *a*, hepatic artery; *d*, hepatic duct.

To take the distribution of the portal vein first:—In its course through the liver this vessel gives off small branches, which divide and subdivide between the lobules surrounding them and limiting them, and from this circumstance called *inter*-lobular veins. From these small vessels a dense capillary network is prolonged into the substance of the lobule, and this network gradually gathering itself up, so to speak, into larger vessels, converges finally to a single small vein, occupying the centre of the lobule, and hence called *intra*-lobular. This arrangement is well seen in fig. 86, which represents a transverse section of a lobule. The *smaller* branches of the portal vein being closely surrounded by the lobules, give off directly

*Fig. 86.**

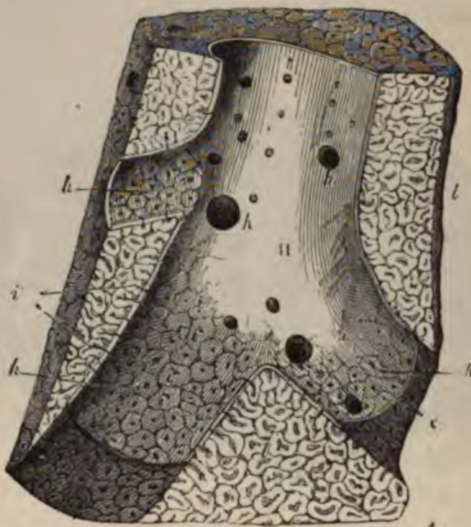
inter-lobular veins (see fig. 85); but here and there, especially where the hepatic artery and duct intervene, branches

* Fig. 86. Cross section of a lobule of the human liver, in which the capillary network between the portal and hepatic veins has been fully injected (from Sappey) $\frac{60}{1}$. 1. Section of the *intra*-lobular vein; 2, its smaller branches collecting blood from the capillary network; 3, *inter*-lobular branches of the vena portæ with their smaller ramifications passing inwards towards the capillary network in the substance of the lobule.

called *vaginal* first arise, and breaking up in the sheath are subsequently distributed like the others around the lobules and become *inter*-lobular. The *larger* trunks of the portal vein being more separated from the lobules by a thicker sheath of Glisson's capsule, give off *vaginal* branches alone, which, however, after breaking up in the sheath, are distributed like the others between the lobules, and become *inter*-lobular veins.

The small *intra*-lobular veins discharge their contents into veins called *sub*-lobular (fig. 88), while these again, by their

Fig. 87.



* Fig. 87. Section of a portion of liver passing longitudinally through a considerable hepatic vein, from the pig (after Kiernan) §. H, hepatic venous trunk, against which the sides of the lobules (*l*) are applied; *h*, *h*, *h*, sublobular hepatic veins, on which the bases of the lobules rest, and through the coats of which they are seen as polygonal figures; *i*, mouth of the intralobular veins, opening into the sublobular veins; *i'*, intralobular veins shown passing up the centre of some divided lobules; *l*, *l*, cut surface of the liver; *c*, *c*, walls of the hepatic venous canal, formed by the polygonal bases of the lobules.

union, form the main branches of the *hepatic* vein, which leaves the posterior border of the liver to end by two or three principal trunks in the inferior vena cava, just before its passage through the diaphragm. The *sub*-lobular and *hepatic veins*, unlike the *portal* vein and its companions, have little or no areolar tissue around them, and their coats being very thin, they form little more than mere channels in the liver substance which closely surrounds them.

Fig. 88.*

The manner in which the lobules are connected with the *sublobular* veins by means of the small *intralobular* veins is well seen in the diagram, fig. 88 and in fig. 87, which represent the parts as seen in a longitudinal section. The appearance has been likened to a twig having leaves without footstalks—the lobules representing the leaves, and the *sublobular* vein the small branch from which it springs. On a transverse section, the appearance of the *intralobular* veins is that of 1, fig. 86, while both a tranverse and longitudinal section are exhibited in fig. 89.

The hepatic artery, the function of which is to distribute blood for nutrition to Glisson's capsule, the walls of the ducts and blood-vessels, and other parts of the liver, is distributed in a very similar manner to the portal vein, its blood being returned by small branches either into the ramifications of the portal vein, or into the capillary plexus of the lobules which connects the *inter-* and *intra*-lobular veins.

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* Fig. 88. Diagram showing the manner in which the lobules of the liver rest on the sublobular veins (after Kiernan).

The hepatic duct divides and subdivides in a manner very like that of the portal vein and hepatic artery, the larger branches being lined by *cylindrical*, and the smaller

Fig. 89*.

by small *polygonal* epithelium. The exact arrangement of its terminal branches, however, and their relation to the liver-cells have not been clearly made out, or, at least, have not been agreed upon by different observers. The chief theories on the subject are three in number:—

1. That the terminal branches of the hepatic duct form an interlobular network, which abuts on the outermost cells of a lobule, but does not enter the inside of the lobule, or only for a little way.

2. That minute branches begin in the lobules *between* the cells, not enclosing them.

3. That the ultimate branches begin in the lobules and enclose hepatic cells.

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* Fig. 89. Capillary network of the lobules of the rabbit's liver (from Kölliker), $\frac{45}{1}$. The figure is taken from a very successful injection of the hepatic veins, made by Harting: it shows nearly the whole of two lobules, and parts of three others; *p*, portal branches running in the interlobular spaces; *h*, hepatic veins penetrating and radiating from the centre of the lobules.

The illustrations below will show the conflicting theories at a glance.

Fig. 90.*

* Fig. 90. Diagrams showing the arrangement of the radicles of the hepatic duct, according to different observers.

1. *d*, *d*, are two branches of the hepatic duct, which is supposed to commence in a plexus situated towards the circumference of the lobule marked *b*, *b*, called by Kiernan the biliary plexus. Within this is seen the central part of the lobule, containing branches of the intralobular vein.

2. A small fragment of an hepatic lobule, of which the smallest intercellular biliary ducts were filled with colouring matter during life, highly magnified (from Chrzonszczewsky).

3. View of some of the smallest biliary ducts illustrating Beale's view of their relation to the biliary cells (from Kölliker after Beale), $\frac{215}{1}$.

The drawing is taken from an injected preparation of the pig's liver;

Functions of the Liver.

The *Secretion of Bile* is the most obvious, and one of the chief functions which the liver has to perform; but, as will be presently shown, it is not the only one; for important changes are effected in certain constituents of the blood in its transit through this gland, whereby they are rendered more fit for their subsequent purposes in the animal economy.

The Bile.

Composition of the Bile.—The bile is a somewhat viscid fluid, of a yellow or greenish-yellow colour, a strongly bitter taste, and when fresh with a scarcely perceptible odour; it has a neutral or slightly alkaline reaction, and its specific gravity is about 1020. Its colour and degree of consistence vary much, apparently independent of disease; but, as a rule, it becomes gradually more deeply coloured and thicker as it advances along its ducts, or when it remains long in the gall-bladder, wherein, at the same time, it becomes more viscid and ropy, of a darker colour, and more bitter taste, mainly from its greater degree of concentration, on account of partial absorption of its water, but partly also from being mixed with mucus.

The following analysis is by Frerichs:—

Composition of Human Bile.

Water	859·2
Solids	140·8
	1,000·0

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a, small branch of an interlobular hepatic duct; *b*, smallest biliary ducts; *c*, portions of the cellular part of the lobule in which the cells are seen within tubes which communicate with the finest ducts.

Biliary acids combined with alkalies	Bilin . .	91·5
Fat		9·2
Cholesterin		2·6
Mucus and colouring matters . .		29·8
Salts		7·7
		140·8

The *Bilin* or *biliary matter* when freed by ether from the fat with which it is combined, is a resinoid substance, soluble in water, alcohol, and alkaline solutions, and giving to the watery solution the taste and general character of bile. It is a compound of soda, with two resinous acids, named glycocholic and taurocholic acids. The former consists of cholic acid conjugated with glycin (or sugar of gelatin), the latter of the same acid conjugated with taurin.

Fatty substances are found in variable proportions. Besides the ordinary saponifiable fats, there is a small quantity of cholesterin (p. 11), which, with the other free fats, is probably held in solution by the tauro-cholate of soda.

A peculiar substance, which Dr. Flint has discovered in the fæces, and named *stercorin* (p. 342), is closely allied to cholesterin; and Dr. Flint believes that while one great function of the liver is to excrete cholesterin from the blood, as the kidney excretes urea, the stercorin of fæces is the modified form in which cholesterin finally leaves the body. Ten grains and a half of stercorin, he reckons, are excreted daily.

Fig. 91.*

The *colouring matter* of the bile has not yet been obtained pure, owing to the facility with which it is decomposed. It occasionally deposits itself in the gall-bladder as a yel-

* Fig. 91. Crystalline scales of cholesterin.

low substance mixed with mucus, and in this state has been frequently examined. It is composed of two colouring matters, called *biliverdin* and *bilifulvin*. By oxidising agencies, as exposure to the air, or the addition of nitric acid, it assumes a dark green colour. In cases of biliary obstruction, it is often re-absorbed, circulates with the blood, and gives to the tissues the yellow tint characteristic of jaundice.

There seems to be some relationship between the colour-matters of the blood and bile, and, it may be added, between these and that of the urine also, so that it is possible they may be, all of them, varieties of the same pigment, or derived from the same source. Nothing, however, is at present certainly known regarding the relation in which one of them stands to the other.

The *mucus* in bile is derived chiefly from the mucous membrane of the gall-bladder, but in part also from the hepatic ducts and their branches. It constitutes the residue after bile is treated with alcohol. The epithelium with which it is mixed may be detected in the bile with the microscope in the form of cylindrical cells, either scattered or still held together in layers. To the presence of this mucus is probably to be ascribed the rapid decomposition undergone by the bilin; for, according to Berzelius, if the mucus be separated, bile will remain unchanged for many days.

The *saline* or *inorganic constituents* of the bile are similar to those found in most other secreted fluids. It is possible that the carbonate and neutral phosphate of sodium and potassium, found in the ashes of bile, are formed in the incineration, and do not exist as such in the fluid. Oxide of iron is said to be a common constituent of the ashes of bile, and copper is generally found in healthy bile, and constantly in biliary calculi.

Such are the principal chemical constituents of bile; but

its physiology is, perhaps, better illustrated by its ultimate elementary composition. According to Liebig's analysis, the biliary matter,—consisting of bilin and the products of its spontaneous decomposition—yields, on analysis, 76 atoms of carbon, 66 of hydrogen, 22 of oxygen, 2 of nitrogen, and a certain quantity of sulphur.* Comparing this with the ultimate composition of the organic parts of blood which may be stated at $C_{48}H_{36}N_6O_{14}$ with sulphur and phosphorus—it is evident that bile contains a large preponderance of carbon and hydrogen, and a deficiency of nitrogen. The import of this will presently appear.

Tests for Bile.—A common test for the presence of bile consists of the addition of a small quantity of nitric acid, when, if bile be present, a play of colours is produced, beginning with green and passing through various tints to red. This test will detect only the *colouring matter* of the bile.

The best test for the *bilin* is Pettenkofer's. To the liquid suspected to contain bile must be added, first, a drop or two of a strong solution of cane-sugar (one part of sugar to four parts of water), and immediately afterwards sulphuric acid, to the extent of about two-thirds of the liquid. On first adding the acid, a whitish precipitate falls; but this redissolves with a slight excess of the acid, and on the further addition of the latter there appears a bright cherry-red colour, gradually changing through a lake tint, to a dark purple.

The *process of secreting bile* is probably continually going on, but appears to be retarded during fasting, and accelerated on taking food. This was shown by Blondlot who,

* The sulphur is combined with the taurin—one of the substances yielded by the decomposition of bilin. According to Dr. Kemp, the sulphur in the bile of the ox, dried and freed from mucus, colouring matter, and salts, constitutes about 3 per cent.

having tied the common bile-duct of a dog, and established a fistulous opening between the skin and gall-bladder, whereby all the bile secreted was discharged at the surface, noticed that when the animal was fasting, sometimes not a drop of bile was discharged for several hours; but that, in about ten minutes after the introduction of food into the stomach, the bile began to flow abundantly, and continued to do so during the whole period of digestion. Bidder and Schmidt's observations are quite in accordance with this.

The bile is probably formed first in the hepatic cells; then, being discharged into the minute hepatic ducts, it passes into the larger trunks, and from the main hepatic duct may be carried at once into the duodenum. But, probably, this happens only while digestion is going on; during fasting it flows from the common bile-duct into the cystic duct, and thence into the gall-bladder, where it accumulates till, in the next period of digestion, it is discharged into the intestine. The gall-bladder thus fulfils what appears to be its chief or only office, that of a reservoir; for its presence enables bile to be constantly secreted for the purification of the blood, yet insures that it shall all be employed in the service of digestion, although digestion is periodic, and the secretion of bile constant.

The mechanism by which the bile passes into the gall-bladder is simple. The orifice through which the common bile-duct communicates with the duodenum is narrower than the duct, and appears to be closed, except when there is sufficient pressure behind to force the bile through it. The pressure exercised upon the bile secreted during the intervals of digestion appears insufficient to overcome the force with which the orifice of the duct is closed; and the bile in the common duct, finding no exit in the intestine, traverses the cystic duct, and so passes into the gall-bladder, being probably aided in this retrograde course by the peri-*staltic* action of the ducts. The bile is discharged from the

gall-bladder, and enters the duodenum on the introduction of food into the small intestine: being pressed on by the contraction of the coats of the gall-bladder, and probably of the common bile-duct also; for both these organs contain organic muscular fibre-cells. Their contraction is excited by the stimulus of the food in the duodenum acting so as to produce a reflex movement, the force of which is sufficient to open the orifice of the common bile-duct.

Various estimates have been made of the *quantity* of bile discharged in the intestines in twenty-four hours: the quantity doubtless varying, like that of the gastric fluid, in proportion to the amount of food taken. A fair average of several computations would give thirty to forty ounces as the quantity daily secreted by man.

The *purposes served by the secretion of bile* may be considered to be of two principal kinds, viz., *excrementitious* and *digestive*.

As an excrementitious substance, the bile serves especially as a medium for the separation of excess of carbon and hydrogen from the blood; and its adaptation to this purpose is well illustrated by the peculiarities attending its secretion and disposal in the fœtus. During intra-uterine life, the lungs and the intestinal canal are almost inactive; there is no respiration of open air or digestion of food; these are unnecessary, because of the supply of well-elaborated nutriment received by the vessels of the fœtus at the placenta. The liver, during the same time, is proportionally larger than it is after birth, and the secretion of bile is active, although there is no food in the intestinal canal upon which it can exercise any digestive property. At birth, the intestinal canal is full of thick bile, mixed with intestinal secretion; for the *meconium*, or fæces of the fœtus, are shown by the analyses of Simon and of Frerichs to contain all the essential principles of bile.

Composition of Meconium (Frerichs):

Biliary resin	15·6
Common fat and cholesterin	15·4
Epithelium, mucus, pigment, and salts	69·
	100·

In the fœtus, therefore, the main purpose of the secretion of bile must be the purification of the blood by *direct* excretion, *i.e.*, by separation from the blood, and ejection from the body without further change. Probably all the bile secreted in fœtal life is incorporated in the meconium, and with it discharged, and thus the liver may be said to discharge a function in some sense vicarious of that of the lungs. For, in the fœtus, nearly all the blood coming from the placenta passes through the liver, previous to its distribution to the several organs of the body; and the abstraction of carbon, hydrogen, and other elements of bile will purify it, as in extra-uterine life it is purified by the separation of carbonic acid and water at the lungs.

The evident disposal of the fœtal bile by excretion, makes it highly probable that the bile in extra-uterine life is also, at least in part, destined to be discharged as excrementitious. But the analysis of the fæces of both children and adults shows that (except when rapidly discharged in purgation) they contain very little of the bile secreted, probably not more than one-sixteenth part of its weight, and that this portion includes only its colouring, and some of its fatty matters, but none of its essential principle, the bilin. All the bilin is again absorbed from the intestines into the blood. But the elementary composition of bilin (see p. 325) shows such a preponderance of carbon and hydrogen, that it cannot be appropriated to the nutrition of the tissues; therefore, it may be presumed that after absorption, the carbon and hydrogen of the bilin combining with oxygen, are excreted as carbonic acid and water. The destination of the bile is, on this

theory, essentially the same in both fœtal and extra-uterine life; only, in the former, it is *directly* excreted, in the latter for the most part *indirectly*, being, before final ejection, modified in its absorption from the intestines, and mingled with the blood.

The change from the direct to the indirect mode of excretion of the bile may, with much probability, be connected with a purpose in relation to the development of heat. The temperature of the fœtus is maintained by that of the parent, and needs no source of heat within the body of the fœtus itself; but, in extra-uterine life, there is (as one may say) a waste of material for heat when any excretion is discharged unoxidized; the carbon and hydrogen of the bilin, therefore, instead of being ejected in the fæces, are re-absorbed, in order that they may be combined with oxygen, and that in the combination, heat may be generated.

From the peculiar manner in which the liver is supplied with much of the blood that flows through it, it is probable, as Dr. Budd suggests, that this organ is excretory, not only for such hydro-carbonaceous matters as may need expulsion from any portion of the blood, but that it serves for the direct purification of the stream which, arriving by the portal vein, has just gathered up various substances in its course through the digestive organs—substances which may need to be expelled, almost immediately after their absorption. For it is easily conceivable that many things may be taken up during digestion, which not only are unfit for purposes of nutrition, but which would be positively injurious if allowed to mingle with the general mass of the blood. The liver, therefore, may be supposed placed in the only road by which such matters can pass into the general current, jealously to guard against their further progress, and turn them back again into an excretory channel. The frequency with which metallic poisons are either excreted by the liver or intercepted and

retained, often for a considerable time, in its own substance, may be adduced as evidence for the probable truth of this supposition.

Though one chief purpose of the secretion of bile may thus appear to be the purification of the blood by ultimate excretion, yet there are many reasons for believing that, while it is in the intestines, it performs an important part in the process of digestion. In nearly all animals, for example, the bile is discharged, not through an excretory duct communicating with the external surface or with a simple reservoir, as most secretions are, but is made to pass into the intestinal canal, so as to be mingled with the chyme directly after it leaves the stomach; an arrangement, the constancy of which clearly indicates that the bile has some important relations to the food with which it is thus mixed. A similar indication is furnished also by the fact that the secretion of bile is most active, and the quantity discharged into the intestines much greater, during digestion than at any other time; although, without doubt, this activity of secretion during digestion may, however, be in part ascribed to the fact that a greater quantity of blood is sent through the portal vein to the liver at this time, and that this blood contains some of the materials of the food absorbed from the stomach and intestines, which may need to be excreted, either temporarily, to be re-absorbed, or permanently.

Respecting the functions discharged by the bile in digestion, there is little doubt that it assists in emulsifying the fatty portions of the food, and thus rendering them capable of being absorbed by the lacteals. For it has appeared in some experiments in which the common bile-duct was tied, that although the process of digestion in the stomach was unaffected, chyle was no longer well-formed; the contents of the lacteals consisting of clear, colourless fluid, instead of being opaque and white, as they ordinarily are, after feeding. (2.) It is probable, also, from the re-

sult of some experiments by Wistinghausen and Hoffmann, that the moistening of the mucous membrane of the intestines by bile may facilitate absorption of fatty matters through it.

(3.) The bile, like the gastric fluid, has a strongly antiseptic power, and may serve to prevent the decomposition of food during the time of its sojourn in the intestines. The experiments of Tiedemann and Gmelin show that the contents of the intestines are much more fœtid after the common bile-duct has been tied than at other times; and the experiments of Bidder and Schmidt on animals with an artificial biliary fistula, confirm this observation; moreover, it is found that the mixture of bile with a fermenting fluid stops or spoils the process of fermentation.

(4.) The bile has also been considered to act as a kind of natural purgative, by promoting an increased secretion of the intestinal glands, and by stimulating the intestines to the propulsion of their contents. This view receives support from the constipation which ordinarily exists in jaundice, from the diarrhœa which accompanies excessive secretion of bile, and from the purgative properties of ox-gall.

Nothing is known with certainty respecting the changes which the re-absorbed portions of the bile undergo, either in the intestines or in the absorbent vessels. That they are much changed appears from the impossibility of detecting them in the blood; and that part of this change is effected in the liver is probable from an experiment of Magendie, who found that when he injected bile into the portal vein a dog was unharmed, but was killed when he injected the bile into one of the systemic vessels.

The secretion of bile, as already observed, is only one of the purposes fulfilled by the liver. Another very important function appears to be that of so acting upon

certain constituents of the blood passing through it, as to render some of them capable of assimilation with the blood generally, and to prepare others for being duly eliminated in the process of respiration. From the labours of M. Bernard, to whom we owe most of what we know on this subject, it appears that the low form of albuminous matter, or albuminose, conveyed from the alimentary canal by the blood of the portal vein, requires to be submitted to the influence of the liver before it can be assimilated by the blood; for if such albuminous matter is injected into the jugular vein, it speedily appears in the urine; but if introduced into the portal vein, and thus allowed to traverse the liver, it is no longer ejected as a foreign substance, but is probably incorporated with the albuminous part of the blood.

An important influence seems also to be exerted by the liver upon the saccharine matters derived from the alimentary canal. The chief purpose of the saccharine and amylaceous principles of food is, probably, in relation to respiration and the production of animal heat; but in order that they may fulfil this, their main office, it seems to be essential that they should undergo some intermediate change, which is effected in the liver, and which consists in their conversion into a peculiar form of saccharine matter, very similar to glucose, or diabetic sugar. That such influence is exerted by the liver seems proved by the fact that when cane sugar is injected into the jugular vein it is speedily thrown out of the system, and appears in the urine; but when injected into the portal vein, and thus enabled to traverse the liver, it ceases to be excreted at the kidneys; and, what is still more to the point, a very large quantity of glucose may be injected into the venous system without any trace of it appearing in the urine. So that it may be concluded, that the saccharine principles of the food undergo, in their passage through the liver, some transformation necessary to the subsequent purpose they

have to fulfil in relation to the respiratory process, and without which, such purpose probably could not be properly accomplished, and the substances themselves would be eliminated as foreign matters by the kidneys.

Then, again, it was discovered by Bernard, and the discovery has been amply confirmed, that the liver possesses the remarkable property of forming glucose or grape-sugar ($C_6H_{12}O_6$), or a substance readily convertible into sugar, even out of principles in the blood which contain no trace of saccharine or amylaceous matter. In Herbivora and in animals living on mixed diet, a large part of the sugar is derived from the saccharine and amylaceous principles introduced in their food. But in animals fed exclusively on flesh, and deprived therefore of this source of sugar, the liver furnishes the means whereby it may be obtained. Not only in Carnivora, however, but apparently in all classes of animals, the liver is continually engaged, during health, in forming sugar, or a substance closely allied to it, in large amount. This substance may always be found in the liver, even when absent from all other parts of the body.

To demonstrate the presence of sugar in the liver, a portion of this organ, after being cut into small pieces, is bruised in a mortar to a pulp with a small quantity of water, and the pulp is boiled with sulphate of soda in order to precipitate albuminous and colouring matters. The decoction is then filtered and may be tested for glucose. The most usual test is Trommer's. To the filtered solution an equal quantity of liquor potassæ is added, with a few drops of a solution of sulphate of copper. The mixture is then boiled, when the presence of sugar is indicated by a reddish-brown precipitate of the suboxide of copper.

The researches of Bernard and others, however, have shown that the sugar is not formed at once at the liver, but that this organ has the power of producing a peculiar substance allied to starch, which is readily convertible into

glucose when in contact with any animal ferment. This substance has received the different names of glycogen, glycogenic substance, animal starch, hepatin.

Glycogen ($C_{12}H_{10}O_{10}$) is obtained by taking a portion of liver from a recently killed animal, and, after cutting it into small pieces, placing it for a short time in boiling water. It is then bruised in a mortar, until it forms a pulpy mass, and subsequently boiled in distilled water for about a quarter of an hour. The glycogen is precipitated from the filtered decoction by the addition of alcohol.

When purified, glycogen is a white, amorphous, starch-like substance, odourless and tasteless, soluble in water, but insoluble in alcohol. It is converted into glucose by boiling with dilute acids, or by contact with any animal ferment.

There are two chief theories concerning the immediate destination of glycogen. (1.) According to Bernard and most other physiologists, its conversion into sugar takes place rapidly during life, and the sugar is conveyed away by the blood of the hepatic veins to be consumed in respiration at the lungs. (2.) Pavy and others believe that the conversion into sugar only occurs after death, and that during life no sugar exists in healthy livers,—the amyloid substance or glycogen being prevented by some force from undergoing the transformation. The chief arguments advanced by Pavy in support of this view are, first, that scarcely a trace of sugar is found in blood drawn during life from the right ventricle, or in blood collected from the right side of the heart immediately after an animal has been suddenly deprived of life, while if the examination be delayed for a little while after death, sugar in abundance may be found in such blood; secondly, that the liver, like the venous blood in the heart, is, at the moment of death, almost completely free from sugar, although afterwards its tissue speedily becomes saccharine, unless the formation of sugar be prevented by freezing, boiling, or

other means calculated to interfere with the action of a ferment on the amyloid substance of the organ. Instead of adopting Bernard's view, that normally, during life, glycogen passes as sugar into the hepatic venous blood, and thereby is conveyed to the lungs to be further disposed of, Pavy inclines to believe that it may represent an intermediate stage in the formation of fat from materials absorbed from the alimentary canal.

For the present we must remain uncertain as to which of these theories contains most truth in it.

Whatever be the destination of this peculiar amyloid substance formed at the liver, most recent observers agree that it is formed at, and exists within, the hepatic cells, from which it may be extracted by the process just described.

Much doubt exists also respecting the mode in which glycogen is formed in the liver, and the materials which furnish its source. Since its quantity is increased after feeding, especially on substances containing much sugar or starch, it is probable that part of it is derived from saccharine principles absorbed from the digestive canal; but since its formation continues even when there is no starch or sugar in the food, the albuminous or fatty principles also have been thought capable of furnishing part of it. Numerous experiments, however, having proved that the liver continues to form sugar in animals after prolonged starvation, and during hybernation, and even after death, its production is clearly independent of the elements of food. One of Bernard's experiments may be quoted in proof of this:—Having fed a healthy dog for many days exclusively on flesh, he killed it, removed the liver at once, and before the contained blood could have coagulated, he thoroughly washed out its tissue by passing a stream of cold water through the portal vein. He continued the injection until the liver was completely exsanguined, until the issuing water contained not a trace

of sugar or albumen, and until no sugar was yielded by portions of the organ cut into slices and boiled in water. Having thus deprived the liver of all saccharine matter, he left it for twenty-four hours, aud on then examining it, found in its tissue a large quantity of soluble sugar, which must clearly have been formed subsequently to the organ being washed, and out of some previously insoluble and non-saccharine substance. This and other experiments led him and others to the conclusion that the formation of the amyloid substance by the liver is the result of a kind of secretion or elaboration out of materials in the solid tissues of the gland—such secretion being probably effected by the hepatic cells, in which, indeed, as already observed, the substance has been detected.

According to this view, then, the liver may be regarded as an organ engaged in forming two kinds of secretion, namely, bile and sugar, or rather, glycogen readily convertible into sugar. The former, chiefly excrementitious, passes along the bile-ducts into the intestines, where it may subserve some purposes in relation to digestion, and is then for the most part re-absorbed, and ultimately eliminated during the processes concerned in the production of animal heat. The latter, namely sugar, being soluble, is, unless Pavy's view be correct, taken up by the blood in the hepatic vein, conveyed through the right side of the heart to the lungs, where it is probably consumed in the respiratory process, and thus contributes to the production of animal heat.

The formation of glycogen or of sugar is, like all other processes in the living body, under the control of the nervous system. Bernard discovered that by pricking the floor of the fourth ventricle, the quantity of sugar formed was so much in excess of the normal quantity, as to be excreted by the kidney, and thus produce the leading symptom of diabetes. Section of the inferior cervical ganglion of the sympathetic nerve also produces diabetes.

The channel by which the influence of the nervous system is conducted in the preceding and similar experiments is not accurately known; no theory having been permanently established, which explains all the facts hitherto observed in connection with the influence of the nervous system on the production of glucose.

Summary of the Changes which take place in the Food during its Passage through the Small Intestine.

In order to understand the changes in the food which occur during its passage through the small intestine, it will be well to refer briefly to the state in which it leaves the stomach through the pylorus. It has been said before, that the chief office of the stomach is not only to mix into an uniform mass all the varieties of food that reach it through the œsophagus, but especially to dissolve the nitrogenous portion by means of the gastric juice. The fatty matters, during their sojourn in the stomach, become more thoroughly mingled with the other constituents of the food taken, but are not yet in a state fit for absorption. The conversion of starch into sugar, which began in the mouth, has been interfered with, although not stopped altogether. The soluble matters—both those which were so from the first, as sugar and saline matter, and those which have been made so by the action of the saliva and gastric juice—have begun to disappear by absorption into the blood-vessels, and the same thing has befallen such fluids as may have been swallowed,—wine, water, etc.

The thin pultaceous chyme, therefore, which, during the whole period of gastric digestion, is being constantly squeezed or strained through the pyloric orifice into the duodenum, consists of albuminous matter, broken down, dissolving and half dissolved, fatty matter, broken down, but not dissolved at all, starch very slowly in process of

conversion into sugar, and as it becomes sugar, also dissolving in the fluids with which it is mixed; while with these are mingled gastric fluid, and fluid that has been swallowed, together with such portions of the food as are not digestible, and will be finally expelled as part of the fæces.

On the entrance of the chyme into the duodenum, it is subjected to the influence of the fluid secreted by Lieberkühn's and Brunn's glands, before described, and to that of the bile and pancreatic juice, which are poured into this part of the intestine.

Without doubt, that part of digestion which it is a chief duty of the small intestine to perform, is the alteration of the fat in such a manner as to make it fit for absorption. And there is no doubt that this change is chiefly effected in the upper part of the small intestine. What is the exact share of the process, however, allotted respectively to the bile, pancreatic secretion, and the secretion of the intestinal glands, is still uncertain. It is most probable, however, that the pancreatic secretion and the bile are the main agents in emulsifying the fat, and that they do this by direct admixture with it. They also promote its absorption by moistening the surface of the villi (p. 331).

During digestion in the small intestine, the villi become turgid with blood, their epithelial cells become filled, by absorption, with fat-globules, which, after minute division, transude into the granular basis of the villus, and thence into the lacteal vessel in the centre, by which they are conveyed along the mesentery to the lymphatic glands, and thence into the thoracic duct. A part of the fat is also absorbed by the blood-vessels of the intestine. The term chyle is sometimes applied to the emulsified contents of the intestine after their admixture with the bile and pancreatic juice; but more strictly to the fluid contained in the lacteal vessels during digestion, which differs from ordinary lymph contained in the same vessels at other times,

chiefly in the greatly increased quantity of fat particles which have been absorbed from the small intestine.

Although the most evident function of the small intestine is the digestion of fat, it must not be forgotten that a great part of the other constituents of the food is by no means completely digested when it leaves the stomach. Indeed, its leaving it unabsorbed would, alone, be proof of this fact.

The *albuminous* substances which have been partly dissolved in the stomach continue to be acted on by the gastric juice which passes into the duodenum with them, and the effect of the last-named secretion is assisted or complemented by that of the pancreas and intestinal glands. As the albuminous matters are dissolved, they are absorbed chiefly by the blood-vessels, and only to a small extent, probably, by the lacteals.

The *starchy*, or amylaceous portion of the food, the conversion of which into dextrin and sugar was more or less interrupted during its stay in the stomach, is now acted on briskly by the secretion of the pancreas, and of Brunn's glands, and perhaps of Lieberkühn's glands also, and the sugar as it is formed dissolves in the intestinal fluids, and afterwards, like the albumen, is absorbed chiefly by the blood-vessels.

The *liquids*, swallowed as such, which may have escaped absorption in the stomach, are absorbed probably very soon after their entrance into the intestine; the fluidity of the contents of the latter being preserved more by the constant secretion of fluid by the intestinal glands, pancreas, and liver, than by any given portion of fluid, whether swallowed or secreted, remaining long unabsorbed. From this fact, therefore, it may be gathered that there is a kind of circulation constantly proceeding from the intestines into the blood, and from the blood into the intestines again; for, as all the fluid, probably a very large amount, secreted by the intestinal glands, must come from the

blood, the latter would be too much drained, were it not that the same fluid after secretion is again re-absorbed into the current of blood—going into the blood charged with nutrient products of digestion—coming out again by secretion through the glands in a comparatively uncharged condition.

It has been said before that the contents of the stomach during gastric digestion have a strongly acid reaction. On the entrance of the chyme into the small intestine, this is gradually neutralized to a greater or less degree by admixture with the bile and other secretions with which it is mixed, and the acid reaction becomes less and less strongly marked as the chyme passes along the canal towards the ileo-cæcal valve.

Thus, all the materials of the food are acted on in the small intestine, and a great portion of the nutrient matter is absorbed—the fat chiefly by the *lacteals*, the other principles, when in a state of solution, chiefly by the *blood-vessels*, but neither, probably, exclusively by one set of vessels. At the lower end of the small intestine, the chyme, still thin and pultaceous, is of a light yellow colour, and has a distinctly fæcal odour. In this state it passes through the ileo-cæcal opening into the large intestine.

Summary of the Process of Digestion in the Large Intestine.

The changes which take place in the chyme after its passage from the *small* into the *large* intestine are probably only the continuation of the same changes that occur in the course of the food's passage through the upper part of the intestinal canal. From the absence of villi, however, we may conclude that absorption, especially of fatty matter, is in great part completed in the small intestine, while, from the still half-liquid, pultaceous consistence of the chyme when it first enters the cæcum, there can be no doubt that the absorption of liquid is not by any means

concluded. The peculiar odour, moreover, which is acquired after a short time by the contents of the large bowel, would seem to indicate the addition to them, in this region, of some special matter, probably excretory. The acid reaction, which had become less and less distinct in the small bowel, again becomes very manifest in the cæcum—probably from acid fermentation processes in some of the materials of the food.

There seems no reason, however, to conclude that any special, 'secondary,' digestive process occurs in the cæcum or in any other part of the large intestine. Probably any constituent of the food which has escaped digestion and absorption in the small bowel may be digested in the large intestine; and the power of this part of the intestinal canal to digest fatty, albuminous, or other matters, may be gathered from the good effects of nutrient enemata, so frequently given when from any cause there is difficulty in introducing food into the stomach. In ordinary healthy digestion, however, the changes which ensue in the chyme after its passage into the large intestine, are mainly the absorption of the more liquid parts, and the addition of the special excretory products which give it the characteristic odour. At the same time, as before said, it is probable that a certain quantity of nutrient matter always escapes digestion in the small intestine, and that this happens more especially when food has been taken in excess, or when it is of such a kind as to be difficult of digestion. Under these circumstances there is no doubt that such changes as were proceeding in it at the lower part of the ileum may go on unchecked in the large bowel,—the process being assisted by the secretion of the numerous tubular glands therein present.

By these means the contents of the large intestine, as they proceed towards the rectum, become more and more solid, and losing their more liquid and nutrient parts, gradually acquire the odour and consistence characteristic

of fæces. After a sojourn of uncertain duration in the rectum, they are finally expelled by the contraction of its muscular coat, aided, under ordinary circumstances, by the contraction of the abdominal muscles.

For a description of the mechanism by which the act of defæcation is accomplished, see p. 223.

The average quantity of solid fæcal matter evacuated by the human adult in twenty-four hours is about five ounces; an uncertain proportion of which consists simply of the undigested or chemically modified residue of the food and the remainder of certain matters which are excreted in the intestinal canal.

Composition of Fæces.

Water	733·00
Solids	267·00
Special excrementitious constituents :—Excretin, excretoleic acid (Marcet), and stercorin (Austin Flint). Salts :—Chiefly phosphate of magnesia and phosphate of lime, with small quantities of iron, soda, lime, and silica. Insoluble residue of the food (chiefly starch, grains, woody tissue, particles of cartilage, and fibrous tissue, undigested muscular fibres or fat, and the like, with insoluble substances accidentally introduced with the food. Mucus, epithelium, altered colouring matter of bile, fatty acids, etc.	267·00

The time occupied by the journey of a given portion of food from the stomach to the anus, varies considerably even in health, and on this account, probably, it is that such different opinions have been expressed in regard to the subject. Dr. Brinton supposes twelve hours to be occupied by the journey of an ordinary meal through the *small* intes-

tine, and twenty-four to thirty-six hours by the passage through the *large* bowel.

On the Gases contained in the Stomach and Intestines.

It need scarcely be remarked that, under ordinary circumstances, the alimentary canal contains a considerable quantity of gaseous matter. Any one who has had occasion, in a post-mortem examination, either to lay open the intestines, or to let out the gas which they contain, must have been struck by the small space afterwards occupied by the bowels, and by the large degree, therefore, in which the gas, which naturally distends them, contributes to fill the cavity of the abdomen. Indeed, the presence of air in the intestines is so constant, and, within certain limits, the amount in health so uniform, that there can be no doubt that its existence here is not a mere accident, but intended to serve a definite and important purpose, although, probably, a mechanical one.

The sources of the gas contained in the stomach and bowels may be thus enumerated—

1. Air introduced in the act of swallowing either food or saliva.

2. Gases developed by the decomposition of alimentary matter, or of the secretions and excretions mingled with it in the stomach and intestines.

3. It is probable that a certain mutual interchange occurs between the gases contained in the alimentary canal, and those present in the blood of the gastric and intestinal blood-vessels; but the conditions of the exchange are not known, and it is very doubtful whether anything like a true and definite secretion of gas from the blood into the intestines or stomach ever takes place. There can be no doubt, however, that the intestines may be the proper excretory organs for many odorous and other substances, either absorbed from the air taken into the lungs

in inspiration, or absorbed in the upper part of the alimentary canal, again to be excreted at a portion of the same tract lower down—in either case assuming rapidly a gaseous form after their excretion, and in this way, perhaps, obtaining a more ready egress from the body.

It is probable that, under ordinary circumstances, the gases of the stomach and intestines are derived chiefly from the second of the sources which have been enumerated.

Tabular Analysis of Gases contained in the Alimentary Canal.

Whence obtained.	Composition by Volume.					
	Oxygen	Nitrog.	Carbon. Acid.	Hydrog	Carburet. Hydrogen.	Sulphuret Hydrogen.
Stomach	11	71	14	4	—	—
Small Intestine .	—	32	30	38	—	
Cæcum	—	66	12	8	13	
Colon	—	35	57	6	8	trace.
Rectum	—	46	43	—	11	
Expelled *per anum*	—	22	41	19	19	$\frac{1}{2}$

The above tabular analysis of the gases contained in the alimentary canal has been quoted from the analyses of Jurine, Magendie, Marchand, and Chevreul by Dr. Brinton, from whose work the above enumeration of the sources of the gas has been also taken.

Movements of the Intestines.

It remains only to consider the manner in which the food and the several secretions mingled with it are moved through the intestinal canal, so as to be slowly subjected to the influence of fresh portions of intestinal secretion, and as slowly exposed to the absorbent power of all the villi and blood-vessels of the mucous membrane. The movement of the intestines is *peristaltic*

or *vermicular*, and is effected by the alternate contractions and dilatations of successive portions of the intestinal coats. The contractions, which may commence at any point of the intestine, extend in a wave-like manner along the tube. In any given portion, the longitudinal muscular fibres contract first, or more than the circular; they draw a portion of the intestine upwards, or, as it were, backwards, over the substance to be propelled, and then the circular fibres of the same portion contracting in succession from above downwards, or, as it were, from behind forwards, press on the substance into the portion next below, in which at once the same succession of actions next ensues. These movements take place slowly, and, in health, are commonly unperceived by the mind; but they are perceptible when they are accelerated under the influence of any irritant.

The movements of the intestines are sometimes retrograde; and there is no hindrance to the backward movement of the contents of the small intestine. But almost complete security is afforded against the passage of the contents of the large into the small intestine by the ileo-cæcal valve. Besides, — the orifice of communication between the ileum and cæcum (at the borders of which orifice are the folds of mucous membrane which form the valve) is encircled with muscular fibres, the contraction of which prevents the undue dilatation of the orifice.

Proceeding from above downwards, the muscular fibres of the large intestine become, on the whole, stronger in direct proportion to the greater strength required for the onward moving of the fæces, which are gradually becoming firmer. The greatest strength is in the rectum, at the termination of which the circular unstriped muscular fibres form a strong band called the *internal* sphincter, while an *external* sphincter muscle with striped fibres is placed rather lower down, and more externally, and holds the orifice close

by a constant slight contraction under the influence of the spinal cord.

The peculiar condition of the sphincter, in relation to the nervous system, will be again referred to. The remaining portion of the intestinal canal is under the direct influence of the sympathetic or ganglionic system, and, indirectly, or more distantly, is subject to the influence of the brain and spinal cord, which influence appears to be, in some degree, transmitted through the vagus nerve. Experimental irritation of the brain or cord produces no evident or constant effect on the movements of the intestines during life; yet in consequence of certain conditions of the mind, the movements are accelerated or retarded; and in paraplegia the intestines appear after a time much weakened in their power, and costiveness, with a tympanitic condition, ensues. Immediately after death, irritation of both the sympathetic and pneumo-gastric nerves, if not too strong, induces genuine peristaltic movements of the intestines. Violent irritation stops the movements. These stimuli act, no doubt, not directly on the muscular tissue of the intestine, but on the rich ganglionic structure shown by Meissner to exist in the sub-mucous tissue. This regulates and controls the movements, and gives to them their peculiar slow, orderly, rhythmic, and peristaltic character, both naturally, and when artifically excited.

CHAPTER X.

ABSORPTION.

The process of absorption has, for one of its objects, the introduction into the blood of fresh materials from the food and air, and of whatever comes into contact with the external or internal surfaces of the body; and, for another, the taking away of parts of the body itself, when, having fulfilled their office, or otherwise requiring removal, they need to be renewed. In both these offices, *i.e.*, in both absorption from without and absorption from within, the process manifests some variety, and a very wide range of action; and in both it is probable that two sets of vessels are, or may be, concerned, namely, the blood-vessels, and the lacteals or lymphatics, to which the term absorbents has been especially applied.

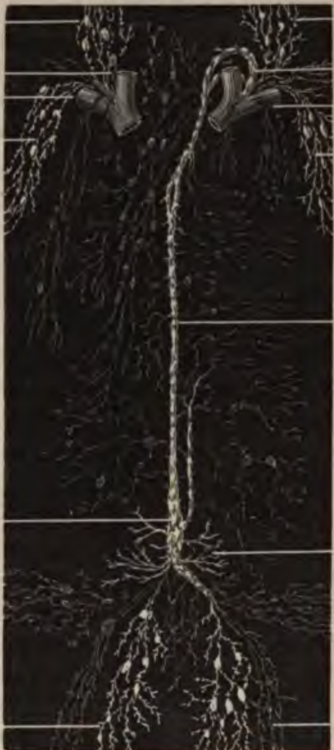
Structure and Office of the Lacteal and Lymphatic Vessels and Glands.

Besides the system of arteries and veins, with their intermediate vessels, the capillaries, there is another system of canals in man and other vertebrata, called the *lymphatic* system, which contains a fluid called *lymph*. Both these systems of vessels are concerned in absorption.

The principal vessels of the lymphatic system are, in structure and general appearance, like very small and thin-walled veins, and like them are provided with valves. By one extremity they commence by fine microscopic branches, the *lymphatic capillaries* or *lymph-capillaries*, in the organs and tissues of nearly every part of the body, and by their other extremities they end directly or indirectly in two trunks which open into the large veins near the heart (fig. 92). Their contents, the *lymph* and *chyle*, unlike the blood,

pass only in one direction, namely, from the fine branches to the trunk and so to the large veins, on entering which they are mingled with the stream of blood, and form part

Fig. 92.*



of its constituents. Remembering the course of the fluid in the lymphatic vessels, viz., its passage in the direction only *towards* the large veins in the neighbourhood of the heart, it will be readily seen from fig. 92 that the greater part of the contents of the lymphatic system of vessels passes

* Fig. 92. Diagram of the principal groups of lymphatic vessels (from Quain).

through a comparatively large trunk called the *thoracic duct*, which finally empties its contents into the blood-stream, at the junction of the internal jugular and subclavian veins of the *left* side. There is a smaller duct on the *right* side. The lymphatic vessels of the intestinal canal are called *lacteals*, because, during digestion, the fluid contained in them resembles milk in appearance; and the *lymph* in the lacteals during the period of digestion is called *chyle*. There is no essential distinction, however, between *lacteals* and *lymphatics*.

In some part of their course all lymphatic vessels pass through certain bodies called *lymphatic glands*.

Lymphatic vessels are distributed in nearly all parts of the body. Their existence, however, has not yet been determined in the placenta, the umbilical cord, the membranes of the ovum, or in any of the non-vascular parts, as the nails, cuticle, hair, and the like.

The lymphatic *capillaries* commence most commonly either in closely-meshed networks, or in irregular lacunar spaces between the various structures of which the different organs are composed. The former is the rule of origin with those lymphatics which are placed most superficially, as, for instance, immediately beneath the skin, or under the mucous and serous membranes; while the latter is most common with those which arise in the substance of organs. In the former instance, their walls are composed of but little more than homogeneous membrane, lined by a single layer of epithelial cells, very similar to those which line the blood-capillaries (fig. 49). In the latter instance the small irregular channels and spaces from which the lymphatics take their origin, although they are formed mostly by the chinks and crannies between the blood-vessels, secreting ducts, and other parts which may happen to form the framework of the organ in which they exist, yet have also a layer of epithelial cells to define and bound them.

The lacteals appear to offer an illustration of anothe mode of origin, namely, in blind dilated extremities (fig

*Fig. 93.**

* Fig. 93. Lymphatic vessels of the head and neck of the uppe part of the trunk (from Mascagni). ⅙.—The chest and pericardium hav been opened on the left side, and the left mamma detached and throw outwards over the left arm, so as to expose a great part of its dee surface. The principal lymphatic vessels and glands are shown on th side of the head and face, and in the neck, axilla, and mediastinum Between the left internal jugular vein and the common carotid artery the upper ascending part of the thoracic duct marked 1, and abov this, and descending to 2, the arch and last part of the duct. Th termination of the upper lymphatics of the diaphragm in the medi astinal glands, as well as the cardiac and the deep mammary lymphatics are also shown.

81, 82); but there is no essential difference in structure between these and the lymphatic capillaries of other parts.

Recent discoveries seem likely to put an end soon to the

Fig. 94.*

Fig. 95†.

* Fig. 94. Superficial lymphatics of the forearm and palm of the hand, ½ (after Mascagni). 5. Two small glands at the bend of the arm. 6. Radial lymphatic vessels. 7. Ulnar lymphatic vessels. 8, 8. Palmar arch of lymphatics. 9, 9'. Outer and inner sets of vessels.

long-standing discussion whether any direct communications exist between the lymph-capillaries and blood-capillaries; the need for any special intercommunicating channels seeming to disappear in the light of more accurate knowledge of the structure and endowments of the parts concerned. For while, on the one hand, the fluid part of the blood constantly exudes or is strained through the walls of the blood-capillaries, so as to moisten all the surrounding tissues, and occupy the interspaces which exist among their different elements, these same interspaces have been shown, as just stated, to form the beginnings of the lymph-capillaries. And while, for many years, the notion of the existence of any such channels between the blood-vessels and lymph-vessels, as would admit blood-corpuscles, has been given up, recent observations have proved that, for the passage of such corpuscles, it is not necessary to assume the presence of any special channels at all, inasmuch as blood-corpuscles can pass bodily, without much difficulty, through the walls of the blood-capillaries and small veins (p. 164), and could pass with still less trouble, probably, through the comparatively ill-defined walls of the capillaries which contain lymph.

Observations of Recklinghausen have led to the discovery that in certain parts of the body openings exist by which lymphatic capillaries directly communicate with parts hitherto supposed to be closed cavities. If the peritoneal cavity be injected with milk, an injection is obtained of the plexus of lymphatic vessels of the central tendon of the diaphragm; and on removing a small portion of the central tendon, with its peritoneal surface uninjured, and

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b. Cephalic vein. *d.* Radial vein. *e.* Median vein. *f.* Ulnar vein. The lymphatics are represented as lying on the deep fascia.

† Fig. 95. Superficial lymphatics of right groin and upper part of thigh, ⅓ (after Mascagni). 1. Upper inguinal glands. 2′. Lower inguinal or femoral glands. 3, 3. Plexus of lymphatics in the course of the long saphenous vein.

examining the process of absorption under the microscope, Recklinghausen noticed that the milk-globules ran towards small natural openings or *stomata* between the epithelial cells, and disappeared by passing vortex-like through them. The *stomata*, which had a roundish outline, were only wide enough to admit two or three milk-globules abreast, and never exceeded the size of an epithelial cell. Openings of a similar kind have been found by Dybskowsky in the pleura; and as they may be presumed to exist in other serous membranes, it would seem as if the serous cavities, hitherto supposed closed, form but a large widening out, so to speak, of the lymph-capillary system with which they directly communicate.

In structure, the medium-sized and larger lymphatic vessels are very like veins; having, according to Kölliker, an external coat of fibro-cellular tissue, with elastic filaments; within this, a thin layer of fibro-cellular tissue, with organic muscular fibres, which have, principally, a circular direction, and are much more abundant in the small than in the larger vessels; and again, within this, an inner elastic layer of longitudinal fibres, and a lining of epithelium; and numerous valves. The valves, constructed like those of veins, and with the free edges turned towards the heart, are usually arranged in pairs, and, in the small vessels, are so closely placed, that when the vessels are full, the valves constricting them where their edges are attached, give them a peculiar braided or knotted appearance (fig. 99).

With the help of the valvular mechanism, all occasional pressure on the exterior of the lymphatic and lacteal vessels propels the lymph towards the heart: thus muscular and other external pressure accelerates the flow of the lymph as it does that of the blood in the veins (see p. 170). The actions of the muscular fibres of the small intestine, and probably the layer of organic muscle present in each intestinal villus (p. 307), seem to assist in propelling the

chyle: for, in the small intestine of a mouse, Poiseuille saw the chyle moving with intermittent propulsions that appeared to correspond with the peristaltic movements of the intestine. But for the general propulsion of the lymph and chyle, it is probable that, together with the *vis a tergo* resulting from absorption (as in the ascent of sap in a tree), and from external pressure, some of the force may be derived from the contractility of the vessel's own walls. Kölliker, after watching the lymphatics in the transparent tail of the tadpole, states that no distinct movements of their walls can ever be seen, but as they are emptied after death they gradually contract, and then, after some time, again dilate to their former size, exactly as the small arteries do under the like circumstances. Thus, also, the larger vessels in the human subject commonly empty themselves after death; so that, although absorption is probably usually going on just before the time of death, it is not common to see the lymphatic or lacteal vessels full. Their power of contraction under the influence of stimuli has been demonstrated by Kölliker, who applied the wire of an electro-magnetic apparatus to some well-filled lymphatics on the skin of a boy's foot, just after the removal of his leg by amputation, and noticed that the calibre of the vessels diminished at least one half. It is most probable that this contraction of the vessels occurs during life, and that it consists, not in peristaltic or undulatory movements, but in an uniform contraction of the successive portions of the vessels, by which pressure is steadily exercised upon their contents, and which alternates with their relaxation.

Lymphatic Glands.

Almost all lymphatic and lacteal vessels in some part of their course pass through one or more small bodies called lymphatic glands (fig 99).

A lymphatic gland is covered externally by a capsule of

connective tissue, which invests and supports the glandular structure within; while prolonged from its inner surface are processes or *trabeculæ* which, entering the gland from all sides, and freely communicating, form a fibrous scaffolding or *stroma* in all parts of the interior. Thus are formed in the outer or *cortical* part of the glands (fig. 96) in the intervals of the trabeculæ, certain intercommunicating spaces termed *alveoli;* while a finer meshwork is formed in the more central or *medullary* part. In the alveoli and the trabecular meshwork the proper gland substance is contained; in the form of nodules in the cortical alveoli, and of rounded cords in the medullary part (fig. 97). The gland-substance of one part is continuous directly or indirectly with that of all others.

*Fig. 96.**

The essential structure of lymphatic-gland substance resembles that which was described as existing, in a simple form, in the interior of the solitary and agminated intestinal follicles (p. 302). Pervading all parts of it, and occupying the alveoli and trabecular spaces before referred to, is a network of the variety of connective tissue termed *retiform* tissue (fig. 98), the interspaces of which are occupied by lymph-corpuscles. The corpuscles are arranged in such a way, that while in the centre of the alveoli and of each mesh they are so crowded together as to be, with the retiform tissue pervading them, a con-

* Fig. 96 (after Kölliker). Section of a mesenteric gland from the ox, slightly magnified. *a*, hilus; *b* (in the central part of the figure), medullary substance; *c*, cortical substance with indistinct alveoli; *d*, capsule.

sistent gland-pulp, continuous in the form of the nodules and cords, before referred to, throughout the whole gland, they are in comparatively small numbers in the outer part of the alveoli and meshes, and leave this portion, as it were, open. (See figs. 97, 98.) This free space between the gland-pulp and the trabecular *stroma*, occupied only by retiform tissue, is called the *lymph-channel* or *lymph-path*, because it is traversed by the lymph, which is continually brought to the gland and conveyed away from it by

Fig. 97.*

lymphatic vessels; those which bring it being termed *afferent* vessels, and those which take it away *efferent* vessels. The former enter the cortical part of the gland and open into its alveoli, at the same time that they lay aside all their coats except the epithelial lining, which may be said to continue to line the lymph-path into which the

* Fig. 97. Section of Medullary Substance of an Inguinal Gland of an Ox (magnified 90 diameters). *a*, *a*, glandular substance or pulp forming rounded cords joining in a continuous net (dark in the figure); *c*, *c*, trabeculæ; the space, *b*, *b*, between these and the glandular substance is the lymph-sinus, washed clear of corpuscles and traversed by filaments of retiform connective tissue (after Kölliker).

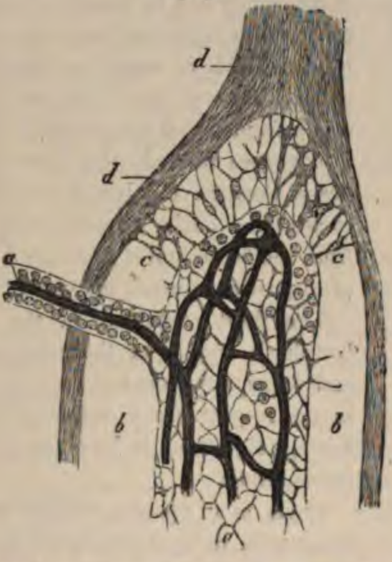
contents of the afferent vessels now pass. The *efferent* vessels begin in the *medullary* part of the gland, and are continuous with the lymph-path here as the *afferent* vessels were with the *cortical* portion; the epithelium of one is continuous with that of the other.

Blood-vessels are freely distributed to the trabecular tissue and to the gland-pulp (fig. 98).

Properties of Lymph and Chyle.

The fluid, or *lymph*, contained in the lymphatic vessels

Fig. 98.*



is, under ordinary circumstances, clear, transparent, and

* Fig. 98. A Small Portion of Medullary Substance from a Mesenteric Gland of the Ox (magnified 300 diameters). *d, d,* trabeculæ; *a,* part of a cord of glandular substances from which all but a few of the lymph-corpuscles have been washed out to show its supporting meshwork of retiform tissue and its capillary blood-vessels (which have been injected, and are dark in the figure); *b, b,* lymph-sinus, of which the retiform tissue is represented only at *c, c* (after Kölliker).

colourless, or of a pale yellow tint. It is devoid of smell, is slightly alkaline, and has a saline taste. As seen with the microscope in the small transparent vessels of the tail of the tadpole, the lymph usually contains no corpuscles or particles of any kind; and it is probably only in the larger trunks in which, by a process similar to that to be described in the chyle, the lymph is more elaborated, that any corpuscles are formed. These corpuscles are similar to those in the chyle, but less numerous. The fluid in which the corpuscles float is commonly and in health albuminous, and contains no fatty particles or molecular base; but it is liable to variations according to the general state of the blood, and that of the organ from which the lymph is derived. As it advances towards the thoracic duct, and passes through the lymphatic glands, it becomes, like chyle, spontaneously coagulable from the formation of fibrin, and the number of corpuscles is much increased.

*Fig. 99.**

The fluid contained in the *lacteals*, or lymphatic vessels of the intestine, is clear and transparent during fasting, and differs in no respect from ordinary lymph; but during digestion, it becomes milky, and is termed *chyle*.

Chyle is an opaque, whitish fluid, resembling milk in appearance, and having a neutral or slightly alkaline reaction. Its whiteness and opacity are due to the presence of innumerable particles of oily or fatty matter, of exceedingly minute though nearly uniform size, measuring on the average about $\frac{1}{30000}$ of an inch (Gulliver). These constitute what Mr. Gulliver appropriately terms the *molecular*

* Fig. 99. A lymphatic gland from the axilla, with its afferent and efferent vessels, injected with mercury (after Bendz).

base of chyle. Their number, and consequently the opacity of the chyle, are dependent upon the quantity of fatty matter contained in the food. Hence, as a rule, the chyle is whitish and most turbid in carnivorous animals; less so in Herbivora; while in birds it is usually transparent. The fatty nature of the molecules is made manifest by their solubility in ether, and, when the ether evaporates, by their being deposited in various-sized drops of oil.* Yet, since they do not run together and form a larger drop, as particles of oil would, it appears very probable that each molecule consists of oil coated over with albumen, in the manner in which, as Ascherson observed, oil always becomes covered when set free in minute drops in an albuminous solution. And this view is supported by the fact, that when water or dilute acetic acid is added to chyle, many of the molecules are lost sight of, and oil-drops appear in their place, as if the investments of the molecules had been dissolved, and their oily contents had run together.

Except these molecules, the chyle taken from the villi or from lacteals near them, contains no other solid or organized bodies. The fluid in which the molecules float is albuminous, and does not spontaneously coagulate, though coagulable by the addition of ether. But as the chyle passes on towards the thoracic duct, and especially while it traverses one or more of the mesenteric glands (propelled by forces which have been described with the structure of the vessels), it is elaborated. The quantity of molecules and oily particles gradually diminishes; cells, to which the name of chyle-corpuscles is given, are developed in it; and by the formation of fibrin, it acquires the property of coagulating spontaneously. The higher in the

* Some of the molecules may remain undissolved by the ether; but this appears to be due to their being defended from the action of the ether by being entangled within the albumen which it coagulates.

thoracic duct the chyle advances, the more is it, in all these respects, developed; the greater is the number of chyle-corpuscles, and the larger and firmer is the clot which forms in it when withdrawn and left at rest. Such a clot is like one of blood, without the red corpuscles, having the chyle-corpuscles entangled in it, and the fatty matter forming a white creamy film on the surface of the serum. But the clot of chyle is softer and moister than that of blood. Like blood, also, the chyle often remains for a long time in its vessels without coagulating, but coagulates rapidly on being removed from them (Bouisson). The existence of fibrin, or of the materials which, by their union form it (p. 65 *et seq.*), is, therefore, certain; its increase appears to be commensurate with that of the corpuscles; and, like them, it is not absorbed as such from the chyme (for no fibrin exists in the chyle in the villi), but is gradually elaborated out of the albumen which chyle, in its earliest condition, contains.

The structure of the chyle-corpuscles was described when speaking of the white corpuscles of the blood, with which they are identical.

From what has been said, it will appear that perfect chyle and lymph are, in essential characters, nearly similar, and scarcely differ, except in the preponderance of fatty matter in the chyle. The comparative analysis of the two fluids obtained from the lacteals and the lymphatics of a donkey is thus given by Dr. Owen Rees:—

	Chyle.	Lymph.
Water	90·237	96·536
Albumen	3·516	1·200
Fibrin	0·370	0·120
Animal extractive	1·565	1·559
Fatty matter	3·601	a trace.
Salts	0·711	0·585
	100·000	100·000

The analyses of Nasse afford an estimate of the rela-

tive compositions of the lymph, chyle, and blood of the horse.*

	Lymph.	Chyle.	Blood.
Water	950·	935·	810·
Corpuscles		4·	92·8
Albumen	39·11	31·	80·
Fibrin		0·75	2·8
Extractive matter	4·88	6·25	5·2
Fatty matter	0·09	15·	1·55
Alkaline salts	5·61	7·	6·7
Phosphate of lime and magnesia, oxide of iron, etc.	0·31	1·	0·95
	1000·	1000·	1000·

The contents of the thoracic duct, including both the lymph and chyle mixed, in an executed criminal, were examined by Dr. Rees, who found them to consist of—

Water	90·48
Albumen and fibrin	7·08
Extractive matter	0·108
Fatty "	0·92
Saline "	0·44

From all these analyses of lymph and chyle, it appears that they contain essentially the same organic constituents that are found in the blood, viz., albumen, fibrin, and fatty matter, the same saline substances, and iron. Their composition differs from that of the blood in degree rather than in kind; they contain a less proportion of all the substances dissolved in the water (see Nasse's analyses, just quoted), and much less fibrin. The fibrin † of lymph, besides being less in quantity, appears to be in a less elaborated state than that of the blood, coagulating less rapidly and less firmly. According to Virchow, it never coagulates, under

* The analysis of the blood differs rather widely from that given at page 78; but if it be erroneous, it is probable that corresponding errors exist in the analysis of the lymph and chyle; and that therefore the tables in the text may represent accurately enough the relation in which the three fluids stand to each other.

† For observations on the nature of fibrin, see p. 65.

ordinary circumstances, within the lymphatic vessels, either during life or after death. These differences gradually diminish, while the lymph and chyle, passing towards and through the thoracic duct, gradually approach the place at which they are to be mingled with the blood. For, in the thoracic duct, besides the higher and more abundant development of the fibrin, the lymph and chyle-corpuscles are found more advanced towards their development into red blood-corpuscles; sometimes even that development is completed, and the lymph has a pinkish tinge from the number of red blood-corpuscles that it contains.

The general result, therefore, of both the microscopic and the chemical examinations of the lymph and chyle, demonstrate that they are rudimental blood; their fluid part being, like the liquor sanguinis, diluted, but gradually becoming more concentrated; and their corpuscles being in process of development into red blood-corpuscles. Thus, in quality, the lymph and chyle are adapted to replenish the blood; and their quantity, so far as it can be estimated, appears ample for this purpose. In one of Magendie's experiments, half an ounce of chyle was collected in five minutes from the thoracic duct of a middle-sized dog; Collard de Martigny obtained nine grains of lymph, in ten minutes, from the thoracic duct of a rabbit which had taken no food for twenty-four hours; and Gieger, from three to five pounds of lymph daily from the foot of a horse, from whom the same quantity had been flowing several years without injury to health. Bidder found, on opening the thoracic duct in cats, immediately after death, that the mingled lymph and chyle continued to flow from one to six minutes; and, from the quantity thus obtained, he estimated that if the contents of the thoracic duct continued to move at the same rate, the quantity which would pass into a cat's blood in twenty-four hours would be equal to about one-sixth of the weight of the whole body. And, since the estimated weight of the blood in cats is to the

weight of their bodies as 1:7, the quantity of lymph daily traversing the thoracic duct would appear to be about equal to the quantity of blood at any time contained in the animals. Schmidt's observations on foals have yielded very similar results. By another series of experiments, Bidder estimated that the quantity of lymph traversing the thoracic duct of a dog in twenty-four hours is about equal to two-thirds of the blood in the body. If we take these estimates, it will not follow from them that the whole of an animal's blood is daily replaced by the development of lymph and chyle; for even if the quantity of lymph and chyle daily formed be equal to that of the blood, the solid contents of the blood will be much too great to be replaced by those of the lymph and chyle. According to Nasse's analyses, the solid matter of a given quantity of blood could not be replaced out of less than three or four times the quantity of lymph and chyle.

Absorption by the Lacteal Vessels.

During the passage of the chyme along the whole tract of the intestinal canal, its completely digested parts are absorbed by the blood-vessels and lacteals distributed in the mucous membrane. The blood-vessels appear to absorb chiefly the dissolved portions of the food, and these, including especially the albuminous and saccharine, they imbibe without choice; whatever can mix with the blood passes into the vessels, as will be presently described. But the lacteals appear to absorb only certain constituents of the food, including particularly the fatty portions. The absorption by both sets of vessels is carried on most actively, but not exclusively, in the villi of the small intestine; for in these minute processes, both the capillary blood-vessels and the lacteals are brought almost into contact with the intestinal contents.

It has been already stated that the villi of the small intestine (figs. 81 and 82), are minute vascular processes

of mucous membrane, each containing a delicate network of blood-vessels and one or more lacteals, and are invested by a sheath of cylindrical epithelium. In the interspaces of the mucous membrane between the villi, as well as over all the rest of the intestinal canal, the lacteals and blood-vessels are also densely distributed in a close network, the lacteals, however, being more sparingly supplied to the large than to the small intestine.

There seems to be no doubt that absorption of fatty matters during digestion, from the contents of the intestines, is effected chiefly by the epithelial cells which line the intestinal tract, and especially by those which clothe the surface of the villi (fig. 81). From these epithelial cells, again, the fatty particles are passed on into the interior of the lacteal vessels (figs. 81 and 82), but how they pass, and what laws govern their so doing, are not at present exactly known.

It is probable that the process of absorption by the epithelial cells, is assisted by the pressure exercised on the contents of the intestines by their contractile walls; and that the absorption of fatty particles is also facilitated by the presence of the bile, the pancreatic and intestinal secretions which moisten the absorbing surface. For it has been found by experiment, that the passage of oil through an animal membrane is made much easier when the latter is impregnated with an alkaline fluid.

Absorption by the Lymphatic Vessels.

The real source of the lymph, and the mode in which its absorption is effected by the lymphatic vessels, were long matters of discussion. But the problem has been much simplified by more accurate knowledge of the anatomical relations of the lymphatic capillaries. It is most probable that the lymph is derived, in great part, from the liquor sanguinis, which, as before remarked, is always exuding from the blood-capillaries into the interstices of

the tissues in which they lie; and changes in the character of the lymph correspond very closely with changes in the character of either the whole mass of blood, or of that in the vessels of the part from which the lymph is examined. Thus Herbst found that the coagulability of the lymph is directly proportionate to that of the blood; and that when fluids are injected into the blood-vessels in sufficient quantity to distend them, the injected substance may be almost directly afterwards found in the lymphatics.

It is not improbable, however, that some other matters than those originally contained in the exuded liquor sanguinis may find their way with it into the lymphatic vessels. Parts which having entered into the composition of a tissue, and, having fulfilled their purpose, require to be removed, may not be altogether excrementitious, but may admit of being re-organised and adapted again for nutrition; and these may be absorbed by the lymphatics, and elaborated with the other contents of the lymph in passing through the glands.

Lymph-Hearts. In reptiles and some birds, an important auxiliary to the movement of the lymph and chyle is supplied in certain muscular sacs, named *lymph-hearts* (fig. 100), and Mr. Wharton Jones has lately shown that the caudal heart of the eel is a lymph-heart also. The number and position of these organs vary. In frogs and toads there are usually four, two anterior and two posterior; in the frog, the posterior lymph-heart on each side is situated in the ischiatic region, just beneath the skin; the anterior lies deeper, just over the transverse process of the third vertebra. Into each of these cavities several lymphatics open, the orifices of the vessels being guarded by valves, which prevent the retrograde passage of the lymph. From each heart a single vein proceeds and conveys the lymph directly into the venous system. In the frog, the inferior lymphatic heart, on each side, pours its lymph into a

branch of the ischiatic vein; by the superior, the lymph is forced into a branch of the jugular vein, which issues from its anterior surface, and which becomes turgid each time that the sac contracts. Blood is prevented from passing from the vein into the lymphatic heart by a valve at its orifice.

Fig. 100.*

The muscular coat of these hearts is of variable thickness; in some cases it can only be discovered by means of the microscope; but in every case it is composed of transversely-striated fibres. The contractions of the hearts are rhythmical, occurring about sixty times in a minute, slowly, and, in comparison with those of the blood-hearts, feebly. The pulsations of the cervical pair are not always synchronous with those of the pair in the ischiatic region, and even the corresponding sacs of opposite sides are not always synchronous in their action.

Unlike the contractions of the blood-heart, those of the lymph-heart appear to be directly dependent upon a certain limited portion of the spinal cord. For Volkmann found that so long as the portion of spinal cord corresponding to the third vertebra of the frog was uninjured, the cervical pair of lymphatic hearts continued pulsating after all the rest of the spinal cord and the brain was destroyed; while destruction of this portion, even though all other

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* Fig. 100. Lymphatic heart (9 lines long, 4 lines broad) of a large species of serpent, the Python bivittatus, (after E. Weber). 4. The external cellular coat. 5. The thick muscular coat. Four muscular columns run across its cavity, which communicates with three lymphatics (1—only one is seen here), with two veins (2, 2). 6. The smooth lining membrane of the cavity. 7. A small appendage, or auricle, the cavity of which is continuous with that of the rest of the organ.

parts of the nervous centres were uninjured, instantly arrested the heart's movements. The posterior or ischiatic pair of lymph-hearts were found to be governed, in like manner, by the portion of spinal cord corresponding to the eighth vertebra. Division of the posterior spinal roots did not arrest the movements; but division of the anterior roots caused them to cease at once.

Absorption by Blood-vessels.

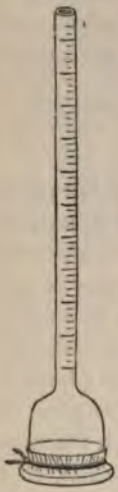
The process thus named is that which has been commonly called *absorption by the veins;* but the term here employed seems preferable, since, though the materials absorbed are commonly found in the veins, this is only because they are carried into them with the circulating blood, after being absorbed by all the blood-vessels (but chiefly by the capillaries) with which they were placed in contact. There is nothing in the mode of absorption by blood-vessels, or in the structure of veins, which can make the latter more active than arteries of the same size, or so active as the capillaries, in the process.

In the absorption by the lymphatics or lacteal vessels just described, there appears something like the exercise of choice in the materials admitted into them. But the absorption by blood-vessels presents no such appearance of selection of materials; rather, it appears, that every substance, whether gaseous, liquid, or a soluble or minutely divided solid, may be absorbed by the blood-vessels, provided it is capable of permeating their walls, and of mixing with the blood; and that of all such substances, the mode and measure of absorption are determined solely by their physical or chemical properties and conditions, and by those of the blood and the walls of the blood-vessels.

The phenomena are, indeed, exactly comparable to that passage of fluids through membrane, which occurs quite independently of vital conditions, and the earliest and best scientific investigation of which was made by Dutrochet.

The instrument which he employed in his experiments was named an endosmometer. It may consist of a graduated tube expanded into an openmouthed bell at one end, over which a portion of membrane is tied (fig. 101). If now the bell be filled with a solution of a salt—say chloride of sodium, and be immersed in water, the water will pass into the solution, and part of the salt will pass out into the water; the water will pass into the solution, much more rapidly than the salt will pass out into the water, and the diluted solution will rise in the tube. To this passage of fluids through membrane the term *Osmosis* is applied.

Fig. 101.



The nature of the membrane used as a septum, and its affinity for the fluids subjected to experiment have an important influence, as might be anticipated, on the rapidity and duration of the osmotic current. Thus, if a piece of ordinary bladder be used as the septum between water and alcohol, the current is almost solely from the water to the alcohol, on account of the much greater affinity of water for this kind of membrane; while, on the other hand, in the case of a membrane of caoutchouc, the alcohol, from its greater affinity for this substance, would pass freely into the water.

Various opinions have been advanced in regard to the nature of the force by which fluids of different chemical composition thus tend to mix through an intervening membrane. According to some, this power is the result of the different degrees of capillary attraction exerted by the pores of the membrane upon the two fluids. Prof. Graham, however, believes that the passage or osmose of water through membrane may be explained by supposing that it combines with the membranous septum, which thus becomes hydrated, and that on reaching the other side it partly leaves the membrane, which thus becomes to a

certain degree de-hydrated. For example, a membrane such as that used in the endosmometer, is hydrated to a higher degree if placed in pure water than in a neutral saline solution. Hence, in the case of the endosmometer filled with the saline solution and placed in water, the equilibrium of hydration is different on the two sides; the outer surface being in contact with pure water tends to hydrate itself in a higher degree than the inner surface does. "When the full hydration of the outer surface extends through the thickness of the membrane, and reaches the inner surface, it there receives a check. The degree of hydration is lowered, and water must be given up by the inner layer of the membrane." Thus the osmose or current of water through the membrane is caused. The passage *outwards* of the saline solution, on the other hand, is not due, probably, to any actual *fluid* current; but to a solution of the salt in successive layers of the water contained in the pores of the membrane, until it reaches the outer surface and *diffuses* in the water there situate.

Thus, "the water movement in osmose is an affair of hydration and of de-hydration in the substance of the membrane or other colloid septum, and the diffusion of the saline solution placed within the osmometer has little or nothing to do with the osmotic result, otherwise than as it affects the state of hydration of the septum."

Prof. Graham has classed various substances according to the degree in which they possess this property of passing, when in a state of solution in water, through membrane; those which pass freely being termed *crystalloids*, and those which pass with difficulty, *colloids*.

This distinction, however, between colloids and crystalloids which is made the basis of their classification, is by no means the only difference between them. The *colloids*, besides the absence of power to assume a crystalline form, are characterised by their inertness as acids or bases, and feebleness in all ordinary chemical relations. Examples of them are found in albumen, gelatin, starch,

hydrated alumina, hydrated silicic acid, etc.; while the *crystalloids* are characterised by qualities the reverse of those just mentioned as belonging to *colloids*. Alcohol, sugar, and ordinary saline substances are examples of *crystalloids*.

Absorption by blood-vessels is the consequence of their walls being, like the membranous septum of the endosmometer, porous and capable of imbibing fluids, and of the blood being so composed that most fluids will mingle with it. The process of absorption, in an instructive, though very imperfect degree, may be observed in any portion of vascular tissue removed from the body. If such an one be placed in a vessel of water, it will shortly swell, and become heavier and moister, through the quantity of water imbibed or soaked into it; and if now, the blood contained in any of its vessels be let out, it will be found diluted with water, which has been absorbed by the blood-vessels and mingled with the blood. The water round the piece of tissue also will become blood-stained; and if all be kept at perfect rest, the stain derived from the solution of the colouring matter of the blood (together with which chemistry would detect some of the albumen and other parts of the liquor sanguinis) will spread more widely every day. The same will happen if the piece of tissue be placed in a saline solution instead of water, or in a solution of colouring or odorous matter, either of which will give their tinge or smell to the blood, and receive, in exchange, the colour of the blood.

Even so simple an experiment will illustrate the absorption by blood-vessels during life; the process it shows is imitated, but with these differences: that, during life, as soon as water or any other substance is admitted into the blood, it is carried from the place at which it was absorbed into the general current of the circulation, and that the colouring matter of the blood is not dissolved so as to ooze out of the blood-vessels into the fluid which they are absorbing.

The absorption of gases by the blood may be thus simply imitated. If venous blood be suspended in a moist bladder in the air, its surface will be reddened by the contact of oxygen, which is first dissolved in the fluid that moistens the bladder, and is then carried in the fluid to the surface of the blood: while, on the other hand, watery vapour and carbonic acid will pass through the membrane, and be exhaled into the air.

In all these cases alike there is a mutual interchange between the substances; while the blood is receiving water, it is giving out its colouring matter and other constituents: or, while it is receiving oxygen, it is giving out carbonic acid and water; so that, at the end of the experiment, the two substances employed in it are mixed; and if, instead of a piece of tissue, one had taken a single blood-vessel full of blood and placed it in the water, both blood and water would, after a time, have been found both inside and outside the vessel. In such a case, moreover, if one were to determine accurately the quantity of water that passed to the blood, and of blood that passed to the water, it would be found that the former was always greater than the latter. And so with other substances; it almost always happens, that if the two liquids placed on opposite sides of a membrane be of different densities or specific gravities, a larger quantity of the less dense fluid passes into the more dense, than of the latter into the former.

The rapidity with which matters may be absorbed from the stomach probably by the blood-vessels chiefly, and diffused through the textures of the body, may be gathered from the history of some experiments by Dr. Bence Jones. From these it appears that even in a quarter of an hour after being given on an empty stomach, chloride of lithium may be diffused into all the vascular textures of the body, and into some of the non-vascular, as the cartilage of the hip-joint, as well as into the aqueous humour of the eye. Into the outer part of the crystalline lens it may pass after a time, varying from half an hour to an hour and a half.

Carbonate of lithia, when taken in five or ten grain doses on an empty stomach, may be detected in the urine in 5 or 10 minutes; or, if the stomach be full at the time of taking the dose, in 20 minutes. It may sometimes be detected in the urine, moreover, for six, seven, or even eight days.

Some experiments on the absorption of various mineral and vegetable poisons, by Mr. Savory, have brought to light the singular fact, that, in some cases, absorption takes place more rapidly from the rectum than from the stomach. Strychnia, for example, when in solution, produces its poisonous effects much more speedily when introduced into the rectum than into the stomach. When introduced in the solid form, however, it is absorbed more rapidly from the stomach than from the rectum, doubtless because of the greater solvent property of the secretion of the former than of that of the latter.

With regard to the degree of absorption by living blood-vessels, much depends on the facility with which the substance to be absorbed can penetrate the membrane or tissue which lies between it and the blood-vessels; for, naturally, the blood-vessels are not bare to absorb. Thus absorption will hardly take place through the epidermis, but is quick when the epidermis is removed, and the same vessels are covered with only the surface of the cutis, or with granulations. In general, the absorption through membranes is in an inverse proportion to the thickness of their epithelia; so Müller found the urinary bladder of a frog traversed in less than a second; and the absorption of poisons by the stomach or lungs appears sometimes accomplished in an immeasurably small time.

The substance to be absorbed must, as a general rule, be in the liquid or gaseous state, or, if a solid, must be soluble in the fluids with which it is brought in contact. Hence the marks of tattooing, and the discoloration produced by nitrate of silver taken internally, remain. Mercury may be absorbed even in the metallic state; and in that state may pass into and remain in the blood-vessels, or be

deposited from them (Oesterlen); and such substances as exceedingly finely-divided charcoal, when taken into the alimentary canal, have been found in the mesenteric veins (Oesterlen); the insoluble materials of ointments may also be rubbed into the blood-vessels; but there are no facts to determine how these various substances effect their passage. Oil, minutely divided, as in an emulsion, will pass slowly into blood-vessels, as it will through a filter moistened with water (Vogel); and, without doubt, fatty matters find their way into the blood-vessels as well as the lymph-vessels of the intestinal canal, although the latter seem to be specially intended for their absorption.

As in the experiments before referred to, the less dense the fluid to be absorbed, the more speedy, as a general rule, is its absorption by the living blood-vessels. Hence the rapid absorption of water from the stomach; also of weak saline solutions; but with strong solutions, there appears less absorption into, than effusion from, the blood-vessels.

The absorption is the less rapid the fuller and tenser the blood-vessels are; and the tension may be so great as to hinder altogether the entrance of more fluid. Thus, Magendie found that when he injected water into a dog's veins to repletion, poison was absorbed very slowly; but when he diminished the tension of the vessels by bleeding, the poison acted quickly. So, when cupping-glasses are placed over a poisoned wound, they retard the absorption of the poison, not only by diminishing the velocity of the circulation in the part, but by filling all its vessels too full to admit more.

On the same ground, absorption is the quicker the more rapid the circulation of the blood; not because the fluid to be absorbed is more quickly imbibed into the tissues, or mingled with the blood, but because as fast as it enters the blood, it is carried away from the part, and the blood, being constantly renewed, is constantly as fit as at the first for the *reception of the* substance to be absorbed.

CHAPTER XI.

NUTRITION AND GROWTH.

NUTRITION or nutritive assimilation is that modification of the formative process peculiar to living bodies by which tissues and organs already formed maintain their integrity. By the incorporation of fresh nutritive principles into their substance, the loss consequent on the waste and natural decay of the component particles of the tissues is repaired; and each elementary particle seems to have the power not only of attracting materials from the blood, but of causing them to assume its structure, and participate in its vital properties.

The relations between development and growth have been already stated (Chap. I.); under the head of NUTRITION will be now considered the process by which parts are maintained in the same general conditions of form, size, and composition, which they have already, by development and growth, attained; and this, notwithstanding continual changes in their component particles. It is by this process that an adult person, in health, is maintained, through a series of some years, with the same general outline of features, the same size and form, and perhaps even the same weight; although, during all this time, the several portions of his body are continually changing: their particles decaying and being removed, and then replaced by the formation of new ones, which, in their turn, also die and pass away. Neither is it only a general similarity of the whole body which is thus maintained. Every organ or part of the body, as much as the whole, exactly maintains its form and composition, as

the issue of the changes continually taking place among its particles.

The change of component particles, in which the nutrition of organs consists, is most evidently shown when, in growth, they maintain their form and other general characters, but increase in size. When, for example, a long bone increases in circumference, and in the thickness of its walls, while, at the same time, its medullary cavity enlarges, it can only be by the addition of materials to its exterior, and a coincident removal of them from the interior of its wall; and so it must be with the growth of even the minutest portions of a tissue. And that a similar change of particles takes place, even while parts retain a perfect uniformity, may be proved, if it can be shown that all the parts of the body are subject to waste and impairment.

In many parts, the removal of particles is evident. Thus, as will be shown when speaking of secretion, the elementary structures composing glands are the parts of which the secretions are composed: each gland is constantly casting off its cells, or their contents, in the secretion which it forms: yet each gland maintains its size and proper composition, because for every cell cast off a new one is produced. So also the epidermis and all such tissues are maintained. In the muscles, it seems nearly certain, that each act of contraction is accompanied with a change in the composition of the contracting tissue, although the change from this cause is less rapid and extensive than was once supposed. Thence, the development of heat in acting muscles, and thence the discharge of urea, carbonic acid, and water—the ordinary products of the decomposition of the animal tissues—which follows all active muscular exercise. Indeed, the researches of Helmholtz almost demonstrate the chemical change that muscles undergo after long-repeated contractions; yet the muscles retain their structure and composition,

because the particles thus changed are replaced by new ones resembling those which preceded them. So again, the increase of alkaline phosphates discharged with the urine after great mental exertion, seems to prove that the various acts of the nervous system are attended with change in the composition of the nervous tissue; yet the condition of that tissue is maintained. In short, for every tissue there is sufficient evidence of impairment in the discharge of its functions: without such change, the production or resistance of physical force is hardly conceivable: and the proof as well as the purpose of the nutritive process appears in the repair or replacement of the changed particles; so that, notwithstanding its losses, each tissue is maintained unchanged.

But besides the impairment and change of composition to which all parts are subject in the discharge of their natural functions, an amount of impairment which will be in direct proportion to their activity, they are all liable to decay and degeneration of their particles, even while their natural actions are not called forth. It may be proved, as Dr. Carpenter first clearly showed, that every particle of the body is formed for a certain period of existence in the ordinary condition of active life; at the end of which period, if not previously destroyed by outward force or exercise, it degenerates and is absorbed, or dies and is cast out.

The simplest examples that can be adduced of this are in the hair and teeth; and it may be observed, that, in the process which will now be described, all the great features of the process of nutrition seem to be represented.*

An eyelash which naturally falls, or which can be drawn

* These and other instances are related more in detail in Mr. Paget's Lectures on Surgical Pathology, from which this chapter was originally written.

out without pain, is one that has lived its natural time, and has died, and been separated from the living parts. In its bulb such an one will be found different from those that are still living in any period of their age. In the early period of the growth of a dark eyelash, the medullary substance appears like an interior cylinder of darker granular substance, continued down to the deepest part, where the hair enlarges to form the bulb. This enlargement, which is of nearly cup-like form, appears to depend on the accumulation of nucleated cells, whose nuclei, according to their position, are either, by narrowing and elongation, to form the fibrous substance of the outer part of the growing and further protruding hair, or are to be transformed into the granular matter of its medullary portion. At the time of early and most active growth, all the cells and nuclei contain abundant pigment-matter, and

Fig. 102.*

* Fig. 102. Intended to represent the changes undergone by a hair towards the close of its period of existence. At A, its activity of growth is diminishing, as shown by the small quantity of pigment contained in the cells of the pulp, and by the interrupted line of dark medullary substance. At B, provision is being made for the formation of a new hair, by the growth of a new pulp connected with the pulp or capsule of the old hair. C. A hair at the end of its period of life, deprived of its sheath and of the mass of cells composing the pulp of a living hair.

the whole bulb looks nearly black. The sources of the material out of which the cells form themselves are at least two; the inner surface of the sheath or capsule, which dips into the skin, enveloping the hair, and the surface of a vascular pulp which fits in a conical cavity in the bottom of the hair-bulb.

Such is the state of parts so long as the growing hair is all dark. But as the hair approaches the end of its existence, instead of the almost sudden enlargement at its bulb, it only swells a little, and then tapers nearly to a point; the conical cavity in its base is contracted; and the cells produced on the inner surface of the capsule contain no pigment. Still, for some time, it continues thus to live and grow; and the vigour of the pulp lasts rather longer than that of the sheath or capsule, for it continues to produce pigment-matter for the medullary substance of the hair after the cortical substance has become white. Thus the column of dark medullary substance appears paler and more slender, and perhaps interrupted, down to the point of the conical pulp which, though smaller, is still distinct, because of the pigment-cells covering its surface.

At length the pulp can be no longer discerned, and uncoloured cells are alone produced, and maintain the latest growth of the hair. With these it appears to grow yet some further distance; for traces of the elongation of their nuclei into fibres appear in lines running from the inner surface of the capsule inwards and along the surface of the hair; and the column of dark medullary substance ceases at some distance above the lower end of the contracted hair-bulb. The end of all is the complete closure of the conical cavity in which the hair-pulp was lodged, the cessation of the production of new cells from the inner surface of the capsule, and the detachment of the hair which, as a dead part, is separated and falls.

Such is the life of a hair, and such its death; which death is spontaneous, independent of exercise, or of any

mechanical external force—the natural termination of a certain period of life. Yet, before the hair dies, provision is made for its successor: for when its growth is failing, there appears below its base a dark spot, the germ or young pulp of the new hair covered with cells containing pigment, and often connected by a series of pigment cells with the old pulp or capsule (fig. 102, B).

Probably there is an intimate analogy between the process of successive life and death, and life communicated to a successor, which is here shown, and that which constitutes the ordinary nutrition of a part. It may be objected, that the death and casting out of the hair cannot be imitated in internal parts; therefore, for an example in which the assumed absorption of the worn-out or degenerate internal particles is imitated in larger organs at the end of their appointed period of life, the instance of the deciduous or milk-teeth may be adduced.

Fig. 103.*

Each milk-tooth is developed from its germ; and in the course of its own development, separates a portion of itself to be the germ of its successor; and each, having reached its perfection, retains for a time its perfect state, and still lives, though it does not grow. But at length, as the new tooth comes, the deciduous tooth dies; or rather its crown dies, and is cast out like the dead hair, while its fang, with its bony sheathing, and vascular and nervous pulp, degenerates and is absorbed (fig. 103). The degeneration is

* Fig. 103. Section of a portion of the upper jaw of a child, showing a new tooth in process of formation, the fang of the corresponding deciduous tooth being absorbed.

accompanied by some unknown spontaneous decomposition of the fang; for it could not be absorbed unless it was first so changed as to be soluble. And it is degeneration, not death, which precedes its removal; for when a tooth-fang dies, as that of the second tooth does in old age, then it is not absorbed, but cast out entire, as a dead part.

Such, or generally such, it seems almost certain, is the process of maintenance by nutrition; the hair and teeth may be fairly taken as types of what occurs in other parts, for they are parts of complex organic structure and composition, and the teeth-pulps, which are absorbed as well as the fangs, are very vascular and sensitive.

Nor are they the only instances that might be adduced. The like development, persistence for a time in the perfect state, death, and discharge, appear in all the varieties of cuticles and gland-cells; and in the epidermis, as in the teeth, there is evidence of decomposition of the old cells, in the fact of the different influence which acetic acid and potash exercise on them and on the young cells. Seeing, then, that the process of nutrition, as thus displayed, both in active organs and in elementary cells, appears in these respects similar, the general conclusion may be that, in nutrition, the ordinary course of each complete elementary organ in the body, after the attainment of its perfect state by development and growth, is to remain in that state for a time; then, independently of the death or decay of the whole body, and in some measure, independently of its own exercise, or exposure to external violence, to die or to degenerate; and then, being cast out or absorbed, to make way for its successor.

It appears, moreover, that the length of life which each part is to enjoy is fixed and determinate, though in some degree subject to accidents and to the expenditure of life in exercise. It is not likely that all parts are made to last a certain and equal time, and then all need to be changed. The bones, for instance, when once completely formed,

must last longer than the muscles and other softer tissues. But when we see that the life of certain parts is of determined length, whether they be used or not, we may assume, from analogy, the same of nearly all.

Now, the deciduous human teeth have an appointed average duration of life. So have the deciduous teeth of all other animals; and in all the numerous instances of moulting, shedding of antlers, of desquamation, change of plumage in birds, and of hair in Mammalia, the only explanation is that these organs have their severally appointed times of living, at the ends of which they degenerate, die, are cast away, and in due time are replaced by others which, in their turn, are to be developed to perfection, to live their life in the mature state, and in their turn to be cast off. So also, in some elementary structures we may discern the same laws of determinate period of life, death, or degeneration, and replacement. They are evident in the history of the blood-corpuscles, both in the superseding of the first set of them by the second at a definite period in the life of the embryo, and in the replacement of those that degenerate by others new-formed from lymph-corpuscles (see p. 92). And if we could suppose the blood-corpuscles grouped together in a tissue instead of floating, we might have in the changes they present an image of the nutrition of the elements of the tissues.

The *duration of life in each particle* is, however, liable to be modified; especially by the exercise of the function of the part. The less a part is exercised the longer do its component particles appear to live: the more active its functions are, the less prolonged is the existence of its individual particles. So in the case of single cells; if the general development of the tadpole be retarded by keeping it in a cold, dark place, and if hereby the function of the blood-corpuscles be slowly and imperfectly discharged, they will maintain their embryonic state for even several weeks later than usual, the development of the second set

of corpuscles will be proportionally postponed, and the individual life of the corpuscles of the first set will be, by the same time, prolonged.

Such being the mode in which the necessity for the process of nutritive maintenance is created, such the sources of impairment and waste of the tissues, the next consideration may be the manner in which the perfect state of a part is maintained by the insertion of new particles in the place of those that are absorbed or cast off.

The process by which a new particle is formed in the place of the old one is probably always a process of development; that is, the cell or fibre, or other element of tissue, passes in its formation through the same stages of development as those elements of the same tissue did which were first formed in the embryo. This is probable from the analogy of the hair, the teeth, the epidermis, and all the tissues that can be observed: in all, the process of repair or replacement is effected through development of the new parts. The existence of nuclei or cytoblasts in nearly all parts that are the seats of active nutrition makes the same probable. For these nuclei, such as are seen so abundant in strong, active muscles, are not remnants of the embryonic tissue, but germs or organs of power for new formation, and their abundance often appears directly proportionate to the activity of growth. Thus, they are always abundant in the fœtal tissues, and those of the young animal; and they are peculiarly numerous in the muscles and the brain, and their disappearance from a part in which they usually exist is a sure accompaniment and sign of degeneration.

A difference may be drawn between what may be called *nutritive reproduction* and *nutritive repetition*. The former is shown in the case of the human teeth. As the deciduous tooth is being developed, a part of its productive capsule is detached, and serves as a germ for the formation of the second tooth; in which second tooth, therefore, the first may be said to be reproduced, in the same sense as that in

which we speak of the organs by which new individuals are formed, as the reproductive organs. But in the shark's jaws, and others, in which we see row after row of teeth succeeding each other, the row behind is not formed of germs derived from the row before: the front row is simply repeated in the second one, the second in the third, and so on. So, in cuticle, the deepest layer of epidermis-cells derives no germs from the layer above: their development is not like a reproduction of the cells that have gone on towards the surface before them: it is only a repetition. It is not improbable that much of the difference in the degree of repair, of which the several tissues are capable after injuries or diseases, may be connected with these differences in their ordinary mode of nutrition.

In order that the process of nutrition may be perfectly accomplished, certain conditions are necessary. Of these, the most important are: 1. A right state and composition of the blood, from which the materials for nutrition are derived. 2. A regular and not far distant supply of such blood. 3. A certain influence of the nervous system. 4. A natural state of the part to be nourished.

1. This *right condition* of the blood does not necessarily imply its accordance with any known standard of composition, common to all kinds of healthy blood, but rather the existence of a certain adaptation between the blood and the tissues, and even the several portions of each tissue. Such an adaptation, peculiar to each individual, is determined in its first formation, and is maintained in the concurrent development and increase of both blood and tissues; and upon its maintenance in adult life appears to depend the continuance of a healthy process of nutrition, or, at least, the preservation of that exact sameness of the whole body and its parts, which constitutes the perfection of nutrition. Some notice of the maintenance of this sameness in the blood has been given already (p. 94), in

speaking of the power of assimilation which the blood exercises, a power exactly comparable with this of maintenance by nutrition in the tissues. And evidence of the adaptation between the blood and the tissues, and of the exceeding fineness of the adjustment by which it is maintained, is afforded by the phenomena of diseases, in which, after the introduction of certain animal poisons, even in very minute quantities, the whole mass of the blood is altered in composition, and the solid tissues are perverted in their nutrition. It is necessary to refer only to such diseases as syphilis, small-pox, and other eruptive fevers, in illustration. And when the absolute dependence of all the tissues on the blood for their very existence is remembered, on the one hand, and, on the other, the rapidity with which substances introduced into the blood are diffused into all, even non-vascular textures (p. 371), it need be no source of wonder that any, even the slightest alteration, from the normal constitution of the blood, should be immediately reflected, so to speak, as a change in the nutrition of the solid tissues and organs which it is destined to nourish.

2. The necessity of *an adequate supply of appropriate blood in or near the part to be nourished*, in order that its nutrition may be perfect, is shown in the frequent examples of atrophy of parts to which too little blood is sent, of mortification or arrested nutrition when the supply of blood is entirely cut off, and of defective nutrition when the blood is stagnant in a part. That the nutrition of a part may be perfect, it is also necessary that the blood should be brought sufficiently near to it for the elements of the tissue to imbibe, through the walls of the blood-vessels, the nutritive materials which they require. The blood-vessels themselves take no share in the process of nutrition, except as carriers of the nutritive matter. Therefore, provided they come so near that this nutritive matter may pass by imbibition into the part to be nourished, it is comparatively immaterial whether they ramify within the substance

of the tissue, or are distributed only on its surface or border.

The blood-vessels serve alike for the nutrition of the vascular and the non-vascular parts, the difference between which, in regard to nutrition, is less than it may seem. For the vascular, the nutritive fluid is carried in streams into the interior; for the non-vascular, it flows on the surface; but in both alike, the parts themselves imbibe the fluid; and although the passage through the walls of the blood-vessels may effect some change in the materials, yet all the process of formation is, in both alike, outside the vessels. Thus, in muscular tissue, the fibrils in the very centre of the fibre nourish themselves: yet these are distant from all blood-vessels, and can only by imbibition receive their nutriment. So, in bones, the spaces between the blood-vessels are wider than in muscle; yet the parts in the meshes nourish themselves, imbibing materials from the nearest source. The non-vascular epidermis, though no vessels pass into its substance, yet imbibes nutritive matter from the vessels of the immediately subjacent cutis, and maintains itself, and grows. The instances of the cornea and vitreous humour are stronger, yet similar; and sometimes even the same tissue is in one case vascular, in the other not, as the osseous tissue, which, when it is in masses or thick layers, has blood-vessels running into it; but when it is in thin layers, as in the lachrymal and turbinated bones, has not. These bones subsist on the blood flowing in the minute vessels of the mucous membrane, from which the epithelium derives nutriment on one side, the bone on the other, and the tissue of the membrane itself on every side: a striking instance how, from the same source, many tissues maintain themselves, each exercising its peculiar assimilative and self-formative power.

3. The third condition said to be essential to a healthy nutrition, is *a certain influence of the nervous system.*

It has been held that the nervous system cannot be

essential to a healthy course of nutrition, because in plants and the early embryo, and in the lowest animals, in which no nervous system is developed, nutrition goes on without it. But this is no proof that in animals which have a nervous system, nutrition may be independent of it; rather, it may be assumed, that in ascending development, as one system after another is added or increased, so the highest (and, highest of all, the nervous system) will always be inserted and blended in a more and more intimate relation with all the rest: according to the general law, that the interdependence of parts augments with their development.

The reasonableness of this assumption is proved by many facts showing the influence of the nervous system on nutrition, and by the most striking of these facts being observed in the higher animals, and especially in man. The influence of the mind in the production, aggravation, and cure of organic diseases is matter of daily observation, and a sufficient proof of influence exercised on nutrition through the nervous system.

Independently of mental influence, injuries either to portions of the nervous centres, or to individual nerves, are frequently followed by defective nutrition of the parts supplied by the injured nerves, or deriving their nervous influence from the damaged portions of the nervous centres. Thus, lesions of the spinal cord are sometimes followed by mortification of portions of the paralysed parts; and this may take place very quickly, as in a case by Sir B. C. Brodie, in which the ankle sloughed within twenty-four hours after an injury of the spine. After such lesions also, the repair of injuries in the paralysed parts may take place less completely than in others; so, Mr. Travers mentions a case in which paraplegia was produced by fracture of the lumbar vertebræ, and, in the same accident, the humerus and tibia were fractured. The former in due time united; the latter did not. The same fact was illus-

trated by some experiments of Dr. Baly, in which having, in salamanders, cut off the end of the tail, and then thrust a thin wire some distance up the spinal canal, so as to destroy the cord, he found that the end of the tail was reproduced more slowly than in other salamanders in whom the spinal cord was left uninjured above the point at which the tail was amputated. Illustrations of the same kind are furnished by the several cases in which division or destruction of the trunk of the trigeminal nerve has been followed by incomplete and morbid nutrition of the corresponding side of the face; ulceration of the cornea being often directly or indirectly one of the consequences of such imperfect nutrition. Part of the wasting and slow degeneration of tissue in paralysed limbs is probably referable also to the withdrawal of nervous influence from them; though, perhaps, more is due to the want of use of the tissues.

Undue irritation of the trunks of nerves, as well as their division or destruction, is sometimes followed by defective or morbid nutrition. To this may be referred the cases in which ulceration of the parts supplied by the irritated nerves occurs frequently, and continues so long as the irritation lasts. Further evidence of the influence of the nervous system upon nutrition is furnished by those cases in which, from mental anguish, or in severe neuralgic headaches, the hair becomes grey very quickly, or even in a few hours.

So many and various facts leave little doubt that the nervous system exercises an influence over nutrition as over other organic processes; and they cannot be explained by supposing that the changes in the nutritive processes are only due to the variations in the size of the blood-vessels supplying the affected parts.

The question remains, through what class of nerves is the influence exerted? When defective nutrition occurs in parts rendered inactive by injury of the motor nerve alone,

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as in the muscles and other tissues of a paralysed face or limb, it may appear as if the atrophy were the direct consequence of the loss of power in the motor nerves; but it is more probable that the atrophy is the consequence of the want of exercise of the parts; for if the muscles be exercised by artificial irritation of their nerves their nutrition will be less defective (J. Reid). The defect of the nutritive process which ensues in the face and other parts, moreover, in consequence of destruction of the trigeminal nerve, cannot be referred to loss of influence of any motor nerves; for the motor-nerves of the face and eye, as well as the olfactory and optic, have no share in the defective nutrition which follows injury of the trigeminal nerve; and one or all of them may be destroyed without any direct disturbance of the nutrition of the parts they severally supply.

It must be concluded, therefore, that the influence which is exercised by nerves over the nutrition of parts to which they are distributed is to be referred either to those among their branches which conduct impressions to the brain and spinal cord, namely, the nerves of common sensation, or, as it is by some supposed, by nerve-fibres, which preside specially over the nutrition of the tissues and organs to which they are supplied. Such special nerves are called *trophic* nerves (see Chapter on the Nervous System).

It is not at present possible to say whether the influence on nutrition is exercised through the cerebro-spinal or through the sympathetic nerves, which, in the parts on which the observation has been made, are generally combined in the same sheath. The truth perhaps is, that it may be exerted through either or both of these nerves. The defect of nutrition which ensues after lesion of the spinal cord alone, the sympathetic nerves being uninjured, and the general atrophy which sometimes occurs in consequence of diseases of the brain, seem to prove the influence of the cerebro-spinal system: while the obser-

vation of Magendie and Mayer, that inflammation of the eye is a constant result of ligature of the sympathetic nerve in the neck, and many other observations of a similar kind, exhibit very well the influence of the latter nerve in nutrition.

4. The fourth condition necessary to healthy nutrition is a healthy state of the part to be nourished. This seems proved by the very nature of the process, which consists in the formation of new parts like those already existing; for, unless the latter are healthy, the former cannot be so. Whatever be the condition of a part, it is apt to be perpetuated by assimilating exactly to itself, and endowing with all its peculiarities, the new particles which it forms to replace those that degenerate. So long as a part is healthy, and the other conditions of healthy nutrition exist, it maintains its healthy condition. But, according to the same law, if the structure of a part be diseased or in any way altered from its natural condition, the alteration is maintained; the altered, like the healthy structure, is perpetuated.

The same exactness of the assimilation of the new parts to the old, which is seen in the nutrition of the healthy tissues, may be observed also in those that are formed in disease. By it, the exact form and relative size of a cicatrix are preserved from year to year; by it, the thickening and induration to which inflammation gives rise are kept up, and the various morbid states of the blood in struma, syphilis, and other chronic diseases are maintained, notwithstanding all diversities of diet. By this precision of the assimilating process, may be explained the law that certain diseases occur only once in the same person, and that certain others are apt to recur frequently; because in both cases alike, the alteration produced by the first attack of the disease is maintained by the exact likeness which the new parts bear to the old ones.

The period, however, during which an alteration of

structure may be exactly maintained by nutrition, is not unlimited; for in nearly all altered parts there appears to exist a tendency to recover the perfect state; and, in many cases, this state is, in time, attained. To this we may attribute the possibility of re-vaccination after the lapse of some years; the occasional recurrence of small-pox, scarlet-fever, and the like diseases, in the same person; the wearing out of scars, and the complete restoration of tissues that have been altered by injury or disease.

Such are some of the more important conditions which appear to be essential to healthy nutrition. Absence or defect of any one of them is liable to be followed by disarrangement of the process; and the various diseases resulting from defective nutrition appear to be due to the failure of these conditions, more often than to imperfection of the process itself.

GROWTH.

Growth, as has been already observed, consists in the increase of a part in bulk and weight by the addition to its substance of particles similar to its own, but more than sufficient to replace those which it loses by the waste or natural decay of its tissue. The structure and composition of the part remain the same; but the increase of healthy tissue which it receives is attended with the capability of discharging a larger amount of its ordinary function.

While development is in progress, growth frequently proceeds with it in the same part, as in the formation of the various organs and tissues of the embryo, in which parts, while they grow larger, are also gradually more developed until they attain their perfect state. But, commonly, growth continues after development is completed, and in some parts, continues even after the full stature of the body is attained, and after nearly every portion

of it has gained its perfect state in both size and composition.

In certain conditions, this continuance or a renewal of growth may be observed in nearly every part of the body. When parts have attained the full size which in the ordinary process of growth they reach, and are then kept in a moderate exercise of their functions, they commonly (as already stated) retain almost exactly the same dimensions through the adult period of life. But when, from any cause, a part already full-grown in proportion to the rest of the body, is called upon to discharge an unusual amount of its ordinary function, the demand is met by a corresponding increase or growth of the part. Illustrations of this are afforded by the increased thickening of cuticle at parts where it is subjected to an unusual degree of occasional pressure or friction, as in the palms of the hands of persons employed in rough manual labour; by the enlargement and increased hardness of muscles that are largely exercised; and by many other facts of a like kind. The increased power of nutrition put forth in such growth is greater than might be supposed; for the immediate effect of increased exercise of a part must be a greater using of its tissue, and might be expected to entail a permanent thinning or diminution of the substance of the part. But the energy with which fresh particles are formed is sufficient not only to replace completely those that are worn away, but to cause an increase in the substance of the part—the amount of this increase being proportioned to the more than usual degree in which its functions are exercised.

The growth of a part from undue exercise of its functions is always, in itself, a healthy process; and the increased size which results from it must be distinguished from the various kinds of enlargement to which the same part may be subject from disease. In the former case, the enlargement is due to an increased quantity of healthy tissue,

providing more than the previous power to meet a particular emergency; the other may be the result of a deposit of morbid material within the natural structure of the part, diminishing, instead of augmenting, its fitness for its office. Such a healthy process of growth in a part, attended with increased power and activity of its functions, may, however, occur as the consequence of disease in some other part; in which case it is commonly called *Hypertrophy*, *i.e.*, excess of nutrition. The most familiar examples of this are in the increased thickness and robustness of the muscular walls of the cavities of the heart in cases of continued obstruction to the circulation; and in the increased development of the muscular coat of the urinary bladder when, from any cause, the free discharge of urine from it is interfered with. In both these cases, though the origin of the growth is the consequence of disease, yet the growth itself is natural, and its end is the benefit of the economy; it is only common growth renewed or exercised in a part which had attained its size in due proportion to the rest of the body.

It may be further mentioned, in relation to the physiology of this subject, that when the increase of function, which is requisite in the cases from which hypertrophy results, cannot be efficiently discharged by mere increase of the ordinary tissue of the part, the development of a new and higher kind of tissue is frequently combined with this growth. An example of this is furnished by the uterus, in the walls of which, when it becomes enlarged by pregnancy, or by the growth of fibrous tumours, organic muscular fibres, found in a very ill-developed condition in its quiescent state, are then enormously developed, and provide for the expulsion of the fœtus or the foreign body. Other examples of the same kind are furnished by cases in which, from obstruction to the discharge of their contents and a consequently increased necessity for propulsive power, the coats of reservoirs and of ducts become the seat

of development of organic muscular fibres, which could be said only just to exist in them before, or were present in a very imperfectly developed condition.

Respecting the mode and conditions of the process of growth, it need only be said, that its mode seems to differ only in degree from that of common maintenance of a part; more particles are removed from, and many more added to a growing tissue, than to one which only maintains itself. But so far as can be ascertained, the mode of removal, the disposition of the removed parts, and the insertion of the new particles, are as in simple maintenance.

The conditions also of growth are the same as those of common nutrition, and are equally or more necessary to its occurrence. When they are very favourable or in excess, growth may occur in the place of common nutrition. Thus hair may grow profusely in the neighbourhood of old ulcers, in consequence, apparently, of the excessive supply of blood to the hair-bulbs and pulps; bones may increase in length when disease brings much blood to them; and, cocks' spurs transplanted from their legs into their combs grow to an unnatural length; the conditions common to all these cases being both an increased supply of blood, and the capability, on the part of the growing tissue, of availing itself of the opportunity of increased absorption and nutrition thus afforded to it. In the absence of the last-named condition, increased supply of blood will not lead to increased nutrition.

CHAPTER XII.

SECRETION.

SECRETION is the process by which materials are separated from the blood, and from the organs in which they are formed, for the purpose either of serving some ulterior office in the economy, or being discharged from the body as excrement. In the former case, both the separated materials and the processes for their separation are termed *secretions;* in the latter, they are named *excretions.*

Most of the secretions consist of substances which, probably, do not pre-exist in the same form in the blood, but require special organs and a process of elaboration for their formation, *e.g.*, the liver for the formation of bile, the mammary gland for the formation of milk. The excretions, on the other hand, commonly or chiefly consist of substances which, as urea, carbonic acid, and probably uric acid, exist ready-formed in the blood, and are merely abstracted therefrom. If from any cause, such as extensive disease or extirpation of an excretory organ, the separation of an excretion is prevented, and an accumulation of it in the blood ensues, it frequently escapes through other organs, and may be detected in various fluids of the body. But this is never the case with secretions; at least with those that are most elaborated; for after the removal of the special organs by which any of them is elaborated, it is no longer formed. Cases sometimes occur in which the secretion continues to be formed by the natural organ, but not being able to escape towards the exterior, on account of some obstruction, is re-absorbed into the blood, and afterwards discharged from it by exudation in other ways; but these are not instances of true vicarious secretion, and must not be thus regarded.

These circumstances, and their final destination, are,

however, the only particulars in which secretions and excretions can be distinguished; for, in general, the structure of the parts engaged in eliminating excretions, *e.g.*, the kidneys, is as complex as that of the parts concerned in the formation of secretions. And since the differences of the two processes of separation, corresponding with those in the several purposes and destinations of the fluids, are not yet ascertained, it will be sufficient to speak in general terms of the process of separation or secretion.

Every secreting apparatus possesses, as essential parts of its structure, a simple and apparently textureless membrane, named the *primary* or *basement-membrane;* certain *cells;* and *blood-vessels.* These three structural elements are arranged together in various ways; but all the varieties may be classed under one or other of two principal divisions, namely, *membranes* and *glands.*

SECRETING MEMBRANES.

The principal secreting membranes are the serous and synovial membranes, the mucous membranes, and the skin.*

Fig. 104.†

The *serous membranes* are formed of fibro-cellular tissue, interwoven so as to constitute a membrane, the free surface of which is covered with a single layer of flattened cells, forming, in most instances, a simple *tesselated epithelium.* Between the epithelium and the subjacent layer of fibro-cellular tissue, is situated the primary or basement membrane (Bowman).

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* The skin will be described in a subsequent chapter.

† Fig. 104. Plan of a secreting membrane: *a*, *membrana propria*, or basement membrane; *b*, ephithelium composed of secreting nucleated cells; *c*, layer of capillary blood-vessels (after Sharpey).

In relation to the process of secretion, the layer of fibro-cellular tissue serves as a ground-work for the ramification of blood-vessels, lymphatics, and nerves. But in its usual form it is absent in some instances, as in the arachnoid covering the dura mater, and in the interior of the ventricles of the brain. The primary membrane and epithelium are probably always present, and are concerned in the formation of the fluid by which the free surface of the membrane is moistened.

The serous membranes are of two principal kinds: *1st.* Those which line visceral cavities,—the arachnoid, pericardium, pleuræ, peritoneum, and tunicæ vaginales. *2nd.* The synovial membranes lining the joints, and the sheaths of tendons and ligaments, with which, also, are usually included the synovial bursæ, or *bursæ mucosæ*, whether these be subcutaneous, or situated beneath tendons that glide over bones.

The serous membranes form closed sacs, and exist wherever the free surfaces of viscera come into contact with each other, or lie in cavities unattached to surrounding parts. The viscera, which are invested by a serous membrane, are, as it were, pressed into the shut sac which it forms, carrying before them a portion of the membrane, which serves as their investment. To the law that serous membranes form shut sacs, there is, in the human subject, one exception, viz.: the opening of the Fallopian tubes into the abdominal cavity,—an arrangement which exists in man and all Vertebrata, with the exception of a few fishes.

The principal purpose of the serous and synovial membranes is to furnish a smooth, moist surface, to facilitate the movements of the invested organ, and to prevent the injurious effects of friction. This purpose is especially manifested in joints, in which free and extensive movements take place; and in the stomach and intestines, which, from the varying quantity and movements of their contents,

are in almost constant motion upon one another and the walls of the abdomen.

The fluid secreted from the free surface of the serous membranes is, in health, rarely more than sufficient to ensure the maintenance of their moisture. The opposed surfaces of each serous sac, are at every point in contact with each other, and leave no space in which fluid can collect. After death, a larger quantity of fluid is usually found in each serous sac; but this, if not the product of manifest disease, is probably such as has transuded after death, or in the last hours of life. An excess of such fluid in any of the serous sacs constitutes dropsy of the sac.

The fluid naturally secreted by the serous membranes appears to be identical, in general and chemical characters, with the serum of the blood, or with very dilute liquor sanguinis. It is of a pale yellow or straw-colour, slightly viscid, alkaline, and, because of the presence of albumen, coagulable by heat. The presence of a minute quantity of fibrin, at least in the dropsical fluids effused into the serous cavities, is shown by their partial coagulation into a jelly-like mass, on the addition of certain animal substances, or on mixture with certain fluids, especially such as contain cells (p. 75 *et seq.*). This similarity of the serous fluid to the liquid part of blood, and to the fluid with which most animal tissues are moistened, renders it probable that it is, in great measure, separated by simple transudation through the walls of the blood-vessels. The probability is increased by the fact that, in jaundice, the fluid in the serous sacs is, equally with the serum of the blood, coloured with the bile. But there is reason for supposing that the fluid of the cerebral ventricles and of the arachnoid sac are exceptions to this rule; for they differ from the fluids of the other serous sacs not only in being pellucid, colourless, and of much less specific gravity, but in that they seldom receive the tinge of bile in the blood, and are not coloured by madder, or other similar substances introduced abundantly into the blood.

It is also probable that the formation of synovial fluid is a process of more genuine and elaborate secretion, by means of the epithelial cells on the surface of the membrane, and especially of those which are accumulated on the edges and processes of the synovial fringes; for, in its peculiar density, viscidity, and abundance of albumen, synovia differs alike from the serum of blood and from the fluid of any of the serous cavities.

The *mucous membranes* line all those passages by which internal parts communicate with the exterior, and by which either matters are eliminated from the body or foreign substances taken into it. They are soft and velvety, and extremely vascular. Their general structure resembles that of serous membranes. It consists of epithelium, basement membrane, and fibro-cellular or areolar tissue containing blood-vessels, lymphatics, and nerves. The structure of mucous membranes is less uniform, especially as regards their epithelium, than that of serous membranes; but the varieties of structure in different parts are described in connection with the organs in which mucous membranes are present, and need not be here noticed in detail. The external surfaces of mucous membranes are attached to various other tissues; in the tongue, for example, to muscle; on cartilaginous parts, to perichondrium; in the cells of the ethmoid bone, in the frontal and sphenoid sinuses, as well as in the tympanum, to periosteum; in the intestinal canal, it is connected with a firm submucous membrane, which on its exterior gives attachment to the fibres of the muscular coat.

The mucous membranes are described as lining certain principal tracts. 1. The *digestive tract* commences in the cavity of the mouth, from which prolongations pass into the ducts of the salivary glands. From the mouth it passes through the fauces, pharynx, and œsophagus, to the stomach, and is thence continued along the whole tract of

the intestinal canal to the termination of the rectum, being in its course arranged in the various folds and depressions already described, and prolonged into the ducts of the pancreas and liver and into the gall-bladder. 2. The *respiratory tract* includes the mucous membrane lining the cavity of the nose, and the various sinuses communicating with it, the lachrymal canal and sac, the conjunctiva of the eye and eyelids, and the prolongation which passes along the Eustachian tubes and lines the tympanum and the inner surface of the membrana tympani. Crossing the pharynx, and lining that part of it which is above the soft palate, the respiratory tract leads into the glottis, whence it is continued, through the larynx and trachea, to the bronchi and their divisions, which it lines as far as the branches of about $\frac{1}{50}$ of an inch in diameter, and continuous with it is a layer of delicate epithelial membrane which extends into the pulmonary cells. 3. The *genito-urinary* tract, which lines the whole of the urinary passages, from their external orifice to the termination of the tubuli uriniferi of the kidneys, extends into and through the organs of generation in both sexes, into the ducts of the glands connected with them; and in the female becomes continuous with the serous membrane of the abdomen at the fimbriæ of the Fallopian tubes.

Along each of the above tracts, and in different portions of each of them, the mucous membrane presents certain structural peculiarities adapted to the functions which each part has to discharge; yet in some essential characters mucous membrane is the same, from whatever part it is obtained. In all the principal and larger parts of the several tracts, it presents, as just remarked, an external layer of epithelium, situated upon *basement-membrane*, and beneath this, a stratum of vascular tissue of variable thickness, which in different cases presents either out-growths in the form of papillæ and villi, or depressions or involutions in the form of glands. But in the prolongations of the tracts, where

they pass into gland-ducts, these constituents are reduced in the finest branches of the ducts to the epithelium, the primary or basement-membrane, and the capillary blood-vessels spread over the outer surface of the latter in a single layer.

The primary or basement-membrane is a thin transparent layer, simple, homogeneous, and with no discernible structure, which on the larger mucous membranes that have a layer of vascular fibro-cellular tissue, may appear to be only the blastema or formative substance, out of which successive layers of epithelium-cells are formed. But in the minuter divisions of the mucous membranes, and in the ducts of glands, it is the layer continuous and correspondent with this basement-membrane that forms the proper walls of the tubes. The cells also which, lining the larger and coarser mucous membranes, constitute their epithelium, are continuous with, and often similar to those which, lining the gland-ducts, are called *gland-cells*, rather than epithelium. Indeed, no certain distinction can be drawn between the epithelium-cells of mucous membranes and gland-cells. In reference to their position, as covering surfaces, they might all be called epithelium-cells, whether they lie on open mucous membranes, or in gland-ducts; and in reference to the process of secretion, they might all be called gland-cells, or at least secreting-cells, since they probably all fulfil a secretory office by separating certain definite materials from the blood and from the part on which they are seated. It is only an artificial distinction which makes them epithelial cells in one place, and gland-cells in another.

It thus appears, that the tissues essential to the production of a secretion are, in their simplest form, a simple membrane, having on one surface blood-vessels, and on the other a layer of cells, which may be called either epithelium-cells or gland-cells. Glands are provided also with lymphatic vessels and nerves. The distribution of

the former is not peculiar, and need not be here considered. Nerve-fibres are distributed both to the blood-vessels of the gland and to its ducts; and, in some glands, it is said, to the secreting cells also.

The structure of the elementary portions of a secreting apparatus, namely epithelium, simple membrane, and blood-vessels, having been already described in this and previous chapters, we may proceed to consider the manner in which they are arranged to form the varieties of *secreting glands.*

SECRETING GLANDS.

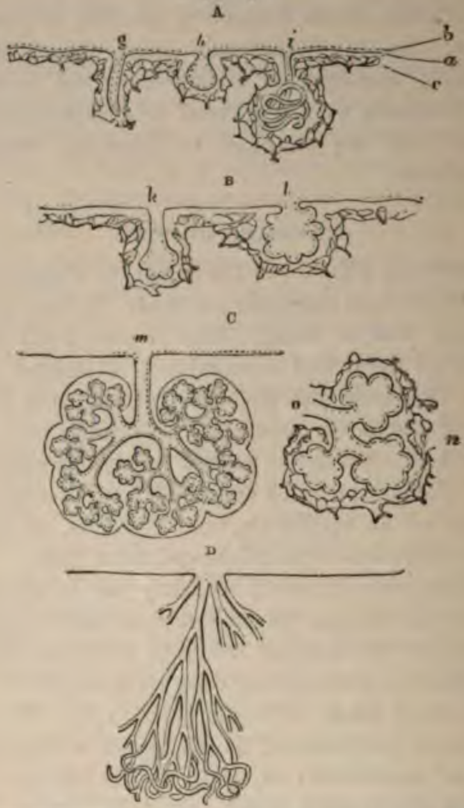
The secreting glands are the organs to which the office of secreting is more especially ascribed: for they appear to be occupied with it alone. They present, amid manifold diversities of form and composition, a general plan of structure, by which they are distinguished from all other textures of the body; especially, all contain, and appear constructed with particular regard to, the arrangement of the cells, which, as already expressed, both line their tubes or cavities as an epithelium, and elaborate, as secreting cells, the substances to be discharged from them.

For convenience of description, they may be divided into three principal groups, the characters of each of which are determined by the different modes in which the sacculi or tubes containing the secreting cells are grouped:—

1. The *simple tubule,* or *tubular gland* (A, fig. 105), examples of which are furnished by the several tubular follicles in mucous membranes: especially by the follicles of Lieberkühn in the mucous membrane of the intestinal canal (p. 300), and the tubular or gastric glands of the stomach (p. 268). These appear to be simple tubular depressions of the mucous membrane on which they open, each consisting of an elongated gland-vesicle, the wall of which is formed of primary membrane, and is lined with secreting cells arranged as an epithelium. To the same class may be

referred the elongated and tortuous sudoriparous glands of the skin (p. 426), and the Meibomian follicles beneath the palpebral conjectiva; though the latter are made more

Fig. 105.*



* Fig. 105. Plans of extension of secreting membrane by inversion or recession in form of cavities. A, simple glands, viz., *g*, straight tube; *h*, sac; *i*, coiled tube. B, multilocular crypts; *k*, of tubular form; *l*, succular. C, racemose, or saccular compound gland; *m*, entire gland, showing branched duct and lobular structure; *n*, a lobule, detached with *o*, branch of duct proceeding from it. D, compound tubular gland (after Sharpey).

complex by the presence of small pouches along their sides (B, fig. 105), and form a connecting link between the members of this division and the next, as the former by their length and tortuosity do between the first division and the third (D, fig. 105).

2. The *aggregated glands*, including those that used to be called *conglomerate*, in which a number of vesicles or *acini* are arranged in groups or lobules (C, fig. 105). Such are all those commonly called mucous glands, as those of the trachea, vagina, and the minute salivary glands. Such, also, are the lachrymal, the large salivary and mammary glands, Brunn's, Cowper's, and Duverney's glands, the pancreas and prostate. These various organs differ from each other only in secondary points of structure; such as, chiefly, the arrangement of their excretory ducts, the grouping of the *acini* and lobules, their connection by fibro-cellular tissue, and supply of blood-vessels. The acini commonly appear to be formed by a kind of fusion of the walls of several vesicles, which thus combine to form one cavity lined or filled with secreting cells which also occupy recesses from the main cavity. The smallest branches of the gland-ducts sometimes open into the centres of these cavities; sometimes the acini are clustered round the extremities, or by the sides of the ducts: but, whatever secondary arrangement there may be, all have the same essential character of rounded groups of vesicles containing gland-cells, and opening, either occasionally or permanently, by a common central cavity into minute ducts, which ducts in the large glands converge and unite to form larger and larger branches, and at length, by one common trunk, open on a free surface of membrane.

3. The *convoluted tubular glands* (D. fig. 105), such as the kidney and testis, form another division. These consist of tubules of membrane, lined with secreting cells arranged like an epithelium. Through nearly the whole of their long course, the tubules present an almost uniform size and

structure; ultimately they terminate either in a cul-de-sac, or by dilating, as in the Malpighian capsules of the kidney, or by forming a simple loop and returning, as in the testicle.

Among these varieties of structure, all the permanent glands are alike in some essential points, besides those which they have in common with all truly secreting structures. They agree in presenting a large extent of secreting surface within a comparatively small space; in the circumstance that while one end of the gland-duct opens on a free surface, the opposite end is always closed, having no direct communication with blood-vessels, or any other canal; and in an uniform arrangement of capillary blood-vessels, ramifying and forming a network around the walls and in the interstices of the ducts and acini.

PROCESS OF SECRETION.

From what has been said, it will have already appeared that the modes in which secretions are produced are at least two. Some fluids, such as the secretions of serous membranes, appear to be simply exudations or oozings from the blood-vessels, whose qualities are determined by those of the liquor sanguinis, while the quantities are liable to variation, or are chiefly dependent on the pressure of the blood on the interior of the blood-vessels. But, in the production of the other secretions, such as those of mucous membranes and all glands, other besides these mechanical forces are in operation. Most of the secretions are indeed liable to be modified by the circumstances which affect the simple exudation from the blood-vessels, and the products of such exudations, when excessive, are apt to be mixed with the more proper products of all the secreting organs. But the act of secretion in all glands is the result of the vital processes of cells or nuclei, which, as they develop themselves and grow, form in their interior the

proper materials of the secretion, and then discharge them.

The best evidence for this view is: *1st.* That cells and nuclei are constituents of all glands, however diverse their outer forms and other characters, and are in all glands placed on the surface or in the cavity whence the secretion is poured. *2nd.* That many secretions which are visible with the microscope may be seen in the cells of their glands before they are discharged. Thus, bile may be often discerned by its yellow tinge in the gland-cells of the liver; spermatozoids in the cells of the tubules of the testicles; granules of uric acid in those of the kidneys of fish; fatty particles, like those of milk, in the cells of the mammary gland.

The process of secretion might, therefore, be said to be accomplished in, and by the life of, these gland-cells. They appear, like the cells or other elements of any other organ, to develop themselves, grow, and attain their individual perfection by appropriating the nutriment from the adjacent blood-vessels and elaborating into the materials of their walls and the contents of their cavities. In this perfected state, they subsist for some brief time, and when that period is over they appear to dissolve or burst and yield themselves and their contents to the peculiar material of the secretion. And this appears to be the case in every part of the gland that contains the appropriate gland-cells; therefore not in the extremities of the ducts or in the acini alone, but in great part of their length.

In these things there is the closest resemblance between secretion and nutrition; for, if the purpose which the secreting glands are to serve in the economy be disregarded, their formation might be considered as only the process of nutrition of organs, whose size and other conditions are maintained in, and by means of, the continual succession of cells developing themselves and passing away. In other words, glands are maintained by the

development of the cells, and their continuance in the perfect state: and the secretions are discharged as the constituent gland-cells degenerate and are set free. The processes of nutrition and secretion are similar, also, in their obscurity: there is the same difficulty in saying why, out of apparently the same materials, the cells of one gland elaborate the components of bile, while those of another form the components of milk, and of a third those of saliva, as there is in determining why one tissue forms cartilage, another bone, a third muscle, or any other tissue. In nutrition, also, as in secretion, some elements of tissues, such as the gelatinous tissues, are different in their chemical properties from any of the constituents ready-formed in the blood. Of these differences, also, no account can be rendered; but, obscure as the cause of these diversities may be, they are not objections to the explanation of secretion as a process similar to nutrition; an explanation with which all the facts of the case are reconcilable.

It may be observed that the diversities presented by the other constituents of glands afford no explanation of the differences or peculiarities of their several products. There are many differences in the arrangements of the blood-vessels in different glands and mucous membranes; and, in accordance with these, much diversity in the rapidity with which the blood traverses them. But there is no reason for believing that these things do more than influence the rate of the process and the quantity of the material secreted. *Cæteris paribus*, the greater the vascularity of a secreting organ, and the larger the supply of blood traversing its vessels in a given time, the larger is the amount of secretion; but there is no evidence that the quantity or mode of movement of the blood can directly determine the quality of the secretion.

The *Discharge of Secretions* from glands may take place as soon as they are formed; or the secretion may be long

retained within the gland or its ducts. The secretions of glands which are continually in active function for the purification of the blood, such as the kidneys, are generally discharged from the gland as rapidly as they are formed. But the secretions of those whose activity of function is only occasional, such as the testicle, are usually retained in the ducts during the periods of the gland's inaction. And there are glands which are like both these classes, such as the lachrymal and salivary, which constantly secrete small portions of fluid, and on occasions of greater excitement discharge it more abundantly.

When discharged into the ducts, the further course of secretions is effected partly by the pressure from behind; the fresh quantities of secretion propelling those that were formed before. In the larger ducts, its propulsion is assisted by the contraction of their walls. All the larger ducts, such as the ureter and common bile-duct, possess in their coats organic muscular fibres; they contract when irritated, and sometimes manifest peristaltic movements. Bernard and Brown-Séquard, indeed, have observed rhythmic contractions in the pancreatic and bile-ducts, and also in the ureters and vasa deferentia. It is probable that the contractile power extends along the ducts to a considerable distance within the substance of the glands whose secretions can be rapidly expelled. Saliva and milk, for instance, are sometimes ejected with much force; doubtless by the energetic and simultaneous contraction of many of the ducts of their respective glands. The contraction of the ducts can only expel the fluid they contain through their main trunk; for at their opposite ends all the ducts are closed.

Circumstances influencing Secretion.—The influence of external conditions on the functions of glands, is manifested chiefly in alterations of the quantity of secretion; and among the principal of these conditions are variations in the quantity of blood, in the quantity of the peculiar

materials for any secretion that it may contain, and in the conditions of the nerves of the glands.

In general, an increase in the quantity of blood traversing a gland, coincides with an augmentation of its secretion. Thus, the mucous membrane of the stomach becomes florid when, on the introduction of food, its glands begin to secrete; the mammary gland becomes much more vascular during lactation; and it appears that all circumstances which give rise to an increase in the quantity of material secreted by an organ, produce, coincidently, an increased supply of blood. In most cases, the increased supply of blood rather follows than precedes the increase of secretion; as, in the nutritive processes, the increased nutrition of a part just precedes and determines the increased supply of blood; but, as also in the nutritive process, an increased supply of blood may have, for a consequence, an increased secretion from the glands to which it is sent.

Glands also secrete with increased activity when the blood contains more than usual of the materials they are designed to separate. Thus, when an excess of urea is in the blood, whether from excessive exercise, or from destruction of one kidney, a healthy kidney will excrete more than it did before. It will, at the same time, grow larger: an interesting fact, as proving both that secretion and nutrition in glands are identical, and that the presence of certain materials in the blood may lead to the formation of structures in which they may be incorporated.

The process of secretion is, also, largely influenced by the condition of the nervous system.

The exact mode in which the nervous system influences secretion must be still regarded as somewhat obscure. In part, it exerts its influence by increasing or diminishing the quantity of blood supplied to the secreting gland, in virtue of the power which it exercises over the contractility of the smaller blood-vessels; while it also has a more direct influence analogous to the *trophic* influence referred to in the

chapter on NUTRITION. Its influence over secretion, as well as over other functions of the body, may be excited by causes acting directly upon the nervous centres, upon the nerves going to the secreting organ, or upon the nerves of other parts. In the latter case, a reflex action is produced: thus the impression produced upon the nervous centres by the contact of food in the mouth, is reflected upon the nerves supplying the salivary glands, and produces, through these, a more abundant secretion of saliva.

Through the nerves, various conditions of the mind also influence the secretions. Thus, the thought of food may be sufficient to excite an abundant flow of saliva. And, probably, it is the mental state which excites the abundant secretion of urine in hysterical paroxysms, as well as the perspirations and, occasionally, diarrhœa, which ensue under the influence of terror, and the tears excited by sorrow or excess of joy. The quality of a secretion may also be affected by the mind; as in the cases in which, through grief or passion, the secretion of milk is altered, and is sometimes so changed as to produce irritation in the alimentary canal of the child, or even death (Carpenter).

The secretions of some of the glands seem to bear a certain relation or antagonism to each other, by which an increased activity of one is usually followed by diminished activity of one or more of the others; and a deranged condition of one is apt to entail a disordered state in the others. Such relations appear to exist among the various mucous membranes: and the close relation between the secretion of the kidney and that of the skin is a subject of constant observation.

CHAPTER XIII.

THE VASCULAR GLANDS; OR GLANDS WITHOUT DUCTS.

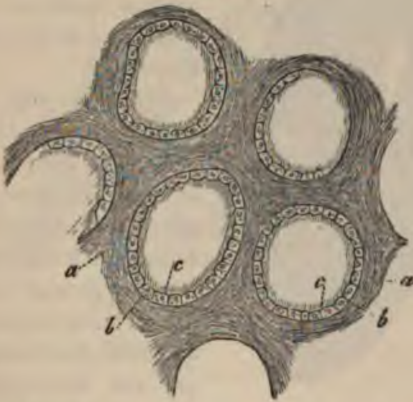
THE materials separated from the blood by the ordinary process of secretion by glands, are always discharged from the organ in which they are formed, and either straightway expelled from the body, or if they are again received into the blood, it is only after they have been altered from their original condition, as in the cases of the saliva and bile. There appears, however, to be a modification of the process of secretion, in which certain materials are abstracted from the blood, undergo some change, and are added to the lymph or restored to the blood, without being previously discharged from the secreting organ, or made use of for any secondary purpose. The bodies in which this modified form of secretion takes place, are usually described as vascular glands, or glands without ducts, and include the spleen, the thymus and thyroid glands, the supra-renal capsules, and, according to Œsterlin and Ecker and Gull, the pineal gland and pituitary body; possibly, also the tonsils.

The solitary and agminate glands of the intestine (p. 302), and lymph-glands in general also closely resemble them; indeed, both in structure and function, the vascular glands bear a close relation, on the one hand, to the true secreting glands, and on the other, to the lymphatic glands.

The evidence in favour of the view that these organs exercise a function analogous to that of secreting glands, has been chiefly obtained from investigations into their structure, which have shown that most of the glands without ducts contain the same essential structures as the secreting glands, except the ducts. They are mainly com-

posed of vesicles, or sacculi, either simple and closed, as in the thyroid (fig. 106), and supra-renal capsules, or variously branched, and with the cavities of the several branches communicating in and by common canals, as in the thymus (fig. 107). These vesicles, like the acini of secreting glands, are formed of a delicate homogeneous membrane, are surrounded with and often traversed by a vascular plexus, and are filled with finely molecular albuminous fluid, suspended in which are either granules of

Fig. 106.*



fat, or cytoblasts or nuclei, or nucleated cells, or a mixture of all these.

Structure of the Spleen.—The spleen is covered externally almost completely by a serous coat derived from the peritoneum, while within this is the proper fibrous coat or capsule of the organ. The latter, composed of connective tissue, with a large preponderance of elastic fibres, forms the immediate investment of the spleen. Prolonged from its inner surface are fibrous processes or *trabeculæ*,

* Fig. 106. Vesicles from the Thyroid Gland of a Child (from Kölliker) $\frac{250}{1}$. *a*, connective tissue between the vesicles; *b*, capsule of the vesicles; *c*, their epithelial lining.

which enter the interior of the organ, and, dividing and anastomosing in all parts, form a kind of supporting framework or *stroma*, in the interstices of which the proper substance of the spleen, or the *spleen-pulp*, is contained. At the *hilus* of the spleen, or the part at which the blood-vessels, nerves, and lymphatics enter, the fibrous coat is prolonged into the spleen-substance in the form of investing sheaths for the arteries and veins, which sheaths again are connected with the *trabeculæ* before referred to.

Fig. 107.*

The *spleen-pulp*, which is a dark red or reddish-brown colour, is composed chiefly of cells. Of these, some are granular corpuscles resembling the lymph-corpuscles, both in general appearance and in being able to perform amœboid movements; others are red blood-corpuscles of normal appearance or variously changed; while there are also large cells containing either pigment allied to the colouring matter of the blood, or rounded corpuscles like red blood-cells.

The splenic artery which enters the spleen by its concave surface or *hilus* divides and subdivides, with but little anastomosis between its branches, in the midst of the spleen-pulp, at the same time that its branches are

* Fig. 107. Transverse Section of a Lobule of an Injected Infantile Thymus Gland (after Kölliker) (magnified 30 diameters). *a*, capsule of connective tissue surrounding the lobule; *b*, membrane of the glandular vesicles; *c*, cavity of the lobule, from which the larger blood-vessels are seen to extend towards and ramify in the spheroidal masses of the lobule.

sheathed, as before said, by the fibrous coat, which they, so to speak, carry into the spleen with them. Ending in capillaries, they either communicate, as in other parts of the body, with the radicles of the veins, or end in lacunar spaces in the spleen-pulp, from which veins arise (Gray).

On the face of a section of the spleen can be usually

Fig. 108.*

seen, readily with the naked eye, minute, scattered, rounded or oval whitish spots, mostly from $\frac{1}{30}$ to $\frac{1}{60}$ inch in diameter. These are the *Malpighian corpuscles* of the spleen, and are situated on the sheaths of the minute splenic arteries, of which, indeed, they may be said to be outgrowths (fig. 108). For while the sheaths of the larger arteries are constructed of ordinary connective tissue, this has become modified where it forms an investment for the

Fig. 108. The figure shows a portion of a small artery, to one of the twigs of which the Malpighian corpuscles are attached.

smaller vessels, so as to be a fine retiform tissue, with abundance of corpuscles, like lymph-corpuscles, contained in its meshes; and the Malpighian corpuscles are but small outgrowths of this *cytogenous* or cell-bearing connective tissue. They are composed of masses of corpuscles, intersected in all parts by a delicate fibrillar tissue, which, though it invests the Malpighian bodies, does not form a complete capsule. Blood-capillaries traverse the Malpighian corpuscles and form a plexus in their interior. The structure of a Malpighian corpuscle of the spleen is, therefore, very similar to that of lymphatic-gland substance (p. 355).

The general resemblances in structure between certain of the vascular glands and the true glands lead to the supposition that both sets of organs pursue, up to a certain point, a similar course in the discharge of their functions. It is assumed that certain principles in an inferior state of organisation are effused from the vessels into the sacculi, and gradually develop into nuclei or cytoblasts, which may be further developed into cells; that in the growth of these nuclei and cells, the materials derived from the blood are elaborated into a higher condition of organization; and that when liberated by the dissolution of these cells, they pass into the lymphatics, or are again received into the blood, whose aptness for nutrition they contribute to maintain.

The opinion that the vascular glands thus serve for the higher organization of the blood, is supported by their being all especially active in the discharge of their functions during fœtal life and childhood, when, for the development and growth of the body, the most abundant supply of highly organized blood is necessary. The bulk of the thymus gland, in proportion to that of the body, appears to bear almost a direct proportion to the activity of the body's

development and growth, and when, at the period of puberty, the development of the body may be said to be complete, the gland wastes, and finally disappears. The thyroid gland and supra-renal capsules, also, though they probably never cease to discharge some amount of function, yet are proportionally much smaller in childhood than in fœtal life and infancy; and with the years advancing to the adult period, they diminish yet more in proportionate size and apparent activity of function. The spleen more nearly retains its proportionate size, and enlarges nearly as the whole body does.

The function of the vascular glands seems not essential to life, at least not in the adult. The thymus wastes and disappears; no signs of illness attend some of the diseases which wholly destroy the structure of the thyroid gland; and the spleen has been often removed in animals, and in a few instances in men, without any evident ill-consequence. It is possible that, in such cases, some compensation for the loss of one of the organs may be afforded by an increased activity of function in those that remain. The experiment, to be complete, should include the removal of all these organs, an operation of course not possible without immediate danger to life. Nor, indeed, would this be certainly sufficient, since there is reason to suppose that the duties of the spleen, after its removal, might be performed by lymphatic glands, between whose structure and that of the vascular glands there is much resemblance, and which, it is said, have been found peculiarly enlarged when the spleen has been removed (Meyer).

Although the functions of all the vascular glands may be similar, in so far as they may all alike serve for the elaboration and maintenance of the blood, yet each of them probably discharges a peculiar office, in relation either to the whole economy, or to that of some other organ. Respecting the special office of the thyroid gland, nothing reasonable can be suggested; nor is there any certain

evidence concerning that of the supra-renal capsules.* Respecting the thymus gland, the observations of Mr. Simon, confirmed by those of Friedleben and others, have shown that in the hybernating animals, in which it exists throughout life, as each successive period of hybernation approaches, the thymus greatly enlarges and becomes laden with fat, which accumulates in it and in fat-glands connected with it, in even larger proportions than it does in the ordinary seats of adipose tissue. Hence it appears to serve for the storing up of materials which, being re-absorbed in inactivity of the hybernating period, may maintain the respiration and the temperature of the body in the reduced state to which they fall during that time.

With respect to the office of the spleen, we have somewhat more definite information. In the first place, the large size which it gradually acquires towards the termination of the digestive process, and the great increase observed about this period in the amount of the finely-granular albuminous plasma within its parenchyma, and the subsequent gradual decrease of this material, seem to indicate that this organ is concerned in elaborating the albuminous or formative materials of food, and for a time storing them up, to be gradually introduced into the blood, according to the demands of the general system. The small amount of fatty matter in such plasma, leads to the inference that the gland has little to do in regard to the preparation of material for the respiratory process.

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* Mr. J. Hutchinson, and, more recently, Dr. Wilks, following out Dr. Addison's discovery, have, by the collection of a large and valuable series of cases in which the supra-renal capsules were diseased, demonstrated most satisfactorily the very close relation subsisting between disease of these organs and brown discoloration of the skin; but the explanation of this relation is still involved in obscurity, and consequently does not aid much in determining the functions of the supra-renal capsules.

Then again, it seems not improbable that, as Hewson originally suggested, the spleen, and perhaps to some extent the other vascular glands, are, like the lymphatic glands, engaged in the formation of the germs of subsequent blood-corpuscles. For it seems quite certain, that the blood of the splenic vein contains an unusually large amount of white corpuscles; and in the disease termed leucocythæmia, in which the pale corpuscles of the blood are remarkably increased in number, there is almost always found an hypertrophied state of the spleen or thyroid body, or some of the lymphatic glands. Accordingly there seems to be a close analogy in function between the so-called vascular and the lymphatic glands: the former elaborating albuminous principles, and forming the germs of new blood-corpuscles out of alimentary materials absorbed by the blood-vessels; the latter discharging the like office on nutritive materials taken up by the general absorbent system. In Kölliker's opinion, the development of colourless and also coloured corpuscles of the blood is one of the essential functions of the spleen, into the veins of which the new-formed corpuscles pass, and are thus conveyed into the general current of the circulation.

There is reason to believe, too, that in the spleen many of the red corpuscles of the blood, those probably which have discharged their office and are worn out, undergo disintegration; for in the coloured portion of the spleen-pulp an abundance of such corpuscles, in various stages of degeneration, are found, while the red corpuscles in the splenic venous blood are said to be relatively diminished. According to Kölliker's description of this process of disintegration, the blood-corpuscles, becoming smaller and darker, collect together in roundish heaps, which may remain in this condition, or become each surrounded by a cell-wall. The cells thus produced may contain from one to twenty blood-corpuscles in their interior. These corpuscles become smaller and smaller; exchange their red

for a golden yellow, brown, or black colour; and, at length, are converted into pigment-granules, which by degrees become paler and paler, until all colour is lost. The corpuscles undergo these changes whether the heaps of them are enveloped by a cell-wall or not.

Besides these, its supposed direct offices, the spleen is believed to fulfil some purpose in regard to the portal circulation, with which it is in close connection. From the readiness with which it admits of being distended, and from the fact that it is generally small while gastric digestion is going on, and enlarges when that act is concluded, it is supposed to act as a kind of vascular reservoir, or diverticulum to the portal system, or more particularly to the vessels of the stomach. That it may serve such a purpose is also made probable by the enlargement which it undergoes in certain affections of the heart and liver, attended with obstruction to the passage of blood through the latter organ, and by its diminution when the congestion of the portal system is relieved by discharges from the bowels, or by the effusion of blood into the stomach. This mechanical influence on the circulation, however, can hardly be supposed to be more than a very subordinate part of the office of an organ of so great complexity as the spleen, and containing so many other structures besides blood-vessels. The same may also be said with regard to the opinion that the thyroid gland is important as a diverticulum for the cerebral circulation, or the thymus for the pulmonary in childhood. These, like the spleen, must have peculiar and higher, though as yet ill-understood, offices.

CHAPTER XIV.

THE SKIN AND ITS SECRETION.

To complete the consideration of the processes of organic life, and especially of those which, by separating materials from the blood, maintain it in the state necessary for the nutrition of the body, the structure and functions of the skin must be now considered: for besides the purposes which it serves—(1), as an external integument for the protection of the deeper tissues, and (2), as a sensitive organ in the exercise of touch, it is also (3), an important excretory, and (4) an absorbing organ; while it plays a most important part in (5) the regulation of the temperature of the body.

Structure of the Skin.

The skin consists, principally, of a layer of vascular tissue, named the *corium, derma,* or *cutis vera,* and an external covering of epithelium termed the *cuticle* or *epidermis.* Within and beneath the corium are imbedded several organs with special functions, namely *sudoriparous* glands, *sebaceous* glands, and *hair-follicles;* and on its surface are sensitive *papillæ.* The so-called appendages of the skin—the *hair* and *nails*—are modifications of the epidermis.

Epidermis.—The *epidermis* is composed of several layers of epithelial cells of the squamous kind (p. 30), the deeper cells, however, being rounded or elongated, and in the latter instance having their long axis arranged vertically as regards the general surface of the skin, while the more

superficial cells are flattened and scaly (fig. 109). The deeper part of the epidermis, which is softer and more opaque than the superficial, is called the *rete mucosum*. Many of the epidermal cells contain pigment, and the varying quantity of this is the source of the different shades of tint in the skin, both of individuals and races. The colouring matter is contained chiefly in the deeper cells composing the *rete mucosum*, and becomes less evident in them as they are gradually pushed up by those under them, and become, like their predecessors, flattened and scale-like (fig. 109). It is by this process of production from beneath, to make up for the waste at the surface, that the growth of the cuticle is effected.

Fig. 109.*

The thickness of the epidermis on different portions of the skin is directly proportioned to the friction, pressure, and other sources of injury to which it is exposed; and the more it is subjected to such injury, within certain limits, the more does it grow, and the thicker and more horny does it become; for it serves as well to protect the sensitive and vascular cutis from injury from without, as to limit the evaporation of fluid from the blood-vessels. The

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* Fig. 109. Skin of the negro, in a vertical section, magnified 250 diameters. *a*, *a*, cutaneous papillæ; *b*, undermost and dark coloured layer of oblong vertical epidermis-cells; *c*, mucous or Malpighian layer; *d*, horny layer (from Sharpey).

adaptation of the epidermis to the latter purposes may be well shown by exposing to the air two dead hands or feet, of which one has its epidermis perfect, and the other is deprived of it; in a day, the skin of the latter will become brown, dry, and horn-like, while that of the former will almost retain its natural moisture.

Cutis vera.—The *corium* or *cutis*, which rests upon a layer of adipose and cellular tissue of varying thickness, is a dense and tough, but yielding and highly elastic structure, composed of fasciculi of fibro-cellular tissue, interwoven in all directions, and forming, by their interlacements, numerous spaces or areolæ. These areolæ are large in the deeper layers of the cutis, and are there usually filled with little masses of fat (fig. 112): but, in the more superficial parts, they are exceedingly small or entirely obliterated.

By means of its toughness, flexibility, and elasticity, the skin is eminently qualified to serve as the general integument of the body, for defending the internal parts from external violence, and readily yielding and adapting itself to their various movements and changes of position. But, from the abundant supply of sensitive nerve-fibres which it receives, it is enabled to fulfil a not less important purpose in serving as the principal organ of the sense of touch. The entire surface of the skin is extremely sensitive, but its tactile properties are due chiefly to the abundant papillæ with which it is studded. These papillæ are conical elevations of the corium, with a single or divided free extremity, more prominent and more densely set at some parts than at others (figs. 110 and 111). The parts on which they are most abundant and most prominent are the palmar surface of the hands and fingers, and the soles of the feet—parts, therefore, in which the sense of touch is most acute. On these parts they are disposed in double rows, in parallel curved lines, separated from each other by depressions (fig. 112). Thus they may

be seen easily on the palm, whereon each raised line is composed of a double row of papillæ, and is intersected by short transverse lines or furrows corresponding with the interspaces between the successive pairs of papillæ. Over other parts of the skin they are more or less thinly scattered, and are scarcely elevated above the surface.

Fig. 110.*

Fig. 111.†

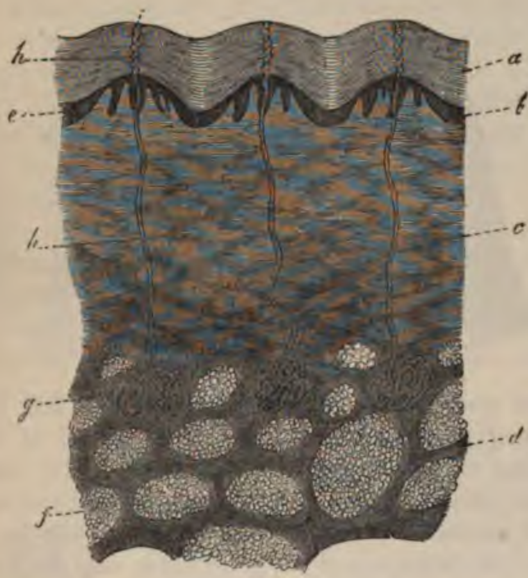
Their average length is about $\frac{1}{100}$th of an inch, and at their base they measure about $\frac{1}{250}$th of an inch in diameter. Each papilla is abundantly supplied with blood, receiving from the vascular plexus in the cutis one or more minute arterial twigs, which divide into capillary loops in its substance, and then reunite into a minute vein, which passes out at its base. The abundant supply of blood which the papillæ thus receive explains the turgescence or kind of erection which they undergo when the circulation through the skin is active. The majority, but not all, of the papillæ contain also one or more terminal nerve-fibres, from the ultimate ramifications of the cutaneous plexus, on which their exquisite sensibility depends. The exact mode in which these nerve-fibres terminate is not yet

* Fig. 110. Papillæ, as seen with a microscope, on a portion of the true skin, from which the cuticle has been removed (after Breschet.)

† Fig. 111. Compound papillæ from the palm of the hand, magnified 60 diameters; *a*, basis of a papilla; *b*, *b*, divisions or branches of the same; *c*, *c*, branches belonging to papillæ, of which the bases are hidden from view (after Kölliker).

satisfactorily determined. In some parts, especially those in which the sense of touch is highly developed, as for example, the palm of the hand and the lips, the fibres

Fig. 112.*

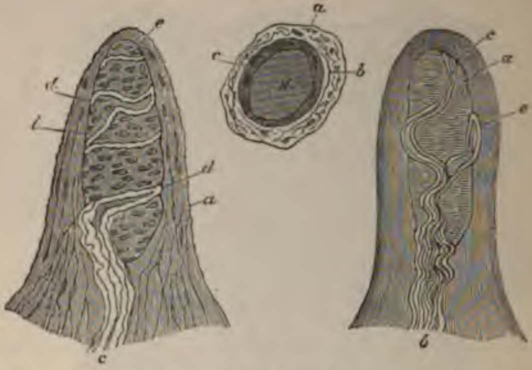


appear to terminate, in many of the papillæ, by one or more free ends in the substance of a dilated oval-shaped body, not unlike a Pacinian corpuscle (figs. 136, 137). occupying the principal part of the interior of the papillæ, and termed a *touch-corpuscle* (fig. 113). The nature of this body is obscure. Kölliker, Huxley, and others, regard it as

* Fig. 112. Vertical section of the skin and subcutaneous tissue, from end of the thumb, across the ridges and furrows, magnified 20 diameters (from Kölliker): *a*, horny, and *b*, mucous layer of the epidermis; *c*, corium; *d*, *panniculus adiposus*; *e*, papillæ on the ridges; *f*, fat clusters; *g*, sweat-glands; *h*, sweat-ducts; *i*, their openings on the surface.

little else than a mass of fibrous or connective tissue, surrounded by elastic fibres, and formed, according to Huxley, by an increased development of the neurilemma of the nerve-fibres entering the papillæ. Wagner, how-

Fig. 113.*



ever, to whom seems to belong the merit of first fully describing these bodies, believes that, instead of thus consisting of a homogeneous mass of connective tissue, they are special and peculiar bodies of laminated structure, directly concerned in the sense of touch. They do not occur in all the papillæ of the parts where they are found, and, as a rule, in the papillæ in which they are present there are no blood-vessels. Since these peculiar bodies in which the nerve-fibres end are only met with in the papillæ of highly sensitive parts, it may be inferred that they are

* Fig. 113. Papillæ from the skin of the hand, freed from the cuticle and exhibiting the tactile corpuscles. Magnified 350 diameters. A. Simple papilla with four nerve-fibres: *a*, tactile corpuscle; *b*, nerves. B. Papilla treated with acetic acid: *a*, cortical layer with cells and fine elastic filaments; *b*, tactile corpuscle with transverse nuclei; *c*, entering nerve with neurilemma or perineurium; *d*, nerve-fibres winding round the corpuscle. C. Papilla viewed from above so as to appear as a cross section: *a*, cortical layer; *b*, nerve-fibre; *c*, sheath of the tactile corpuscle containing nuclei; *d*, core (after Kölliker).

specially concerned in the sense of touch, yet their absence from the papillæ of other tactile parts shows that they are not essential to this sense.

Closely allied in structure to the Pacinian corpuscles and touch-corpuscles are some little bodies about $\frac{1}{800}$ of an inch in diameter, first particularly described by Krause, and named by him "end-bulbs." They are generally oval or spheroidal, and composed externally of a coat of connective tissue enclosing a softer matter, in which the extremity of a nerve terminates. These bodies have been found chiefly in the lips, tongue, palate, and the skin of the glans penis (fig. 114).

Although destined especially for the sense of touch, the papillæ are not so placed as to come into direct contact with external objects; but, like the rest of the surface of the skin, are covered by one or more layers of epithelium, forming the cuticle or epidermis. The papillæ adhere

Fig. 114.*

* Fig. 114. End-bulbs in papillæ (magnified) treated with acetic acid. A, from the lips ; the white loops in one of them are capillaries. B, from the tongue. Two end-bulbs seen in the midst of the simple papillæ : *a*, *a*, nerves (from Kölliker).

very intimately to the cuticle, which is thickest in the spaces between them, but tolerably level on its outer surface: hence, when stripped off from the cutis, as after maceration, its internal surface presents a series of pits and elevations corresponding to the papillæ and their interspaces, of which it thus forms a kind of mould. Besides affording by its impermeability a check to undue evaporation from the skin, and providing the sensitive cutis with a protecting investment, the cuticle is of service in relation to the sense of touch. For, by being thickest in the spaces between the papillæ, and only thinly spread over the summits of these processes, it may serve to subdivide the sentient surface of the skin into a number of isolated points, each of which is capable of receiving a distinct impression from an external body. By covering the papillæ it renders the sensation produced by external bodies more obtuse, and in this manner also is subservient to touch: for unless the very sensitive papillæ were thus defended, the contact of substances would give rise to pain, instead of the ordinary impressions of touch. This is shown in the extreme sensitiveness and loss of tactile power in a part of the skin when deprived of its epidermis. If the cuticle is very thick, however, as on the heel, touch becomes imperfect, or is lost, through the inability of the tactile papillæ to receive impressions through the dense and horny layer covering them.

Sudoriparous Glands.—In the middle of each of the transverse furrows between the papillæ, and irregularly scattered between the bases of the papillæ in those parts of the surface of the body in which there are no furrows between them, are the orifices of ducts of the sudoriparous or sweat glands, by which it is probable that a large portion of the aqueous and gaseous materials excreted by the skin are separated. Each of these glands consists of a small lobular mass, which appears formed of a coil of tubular gland-duct, surrounded by blood-vessels and embedded in

the subcutaneous adipose tissue (fig. 112). From this mass, the duct ascends, for a short distance, in a spiral manner through the deeper part of the cutis, then passing straight, and then sometimes again becoming spiral, it passes through the cuticle and opens by an oblique valve-like aperture. In the parts where the epidermis is thin, the ducts themselves are thinner and more nearly straight in their course (fig. 115). The duct, which maintains nearly the same diameter throughout, is lined with a layer of epithelium continuous with the epidermis; while the part which passes through the epidermis is composed of the latter structure only; the cells which immediately form the boundary of the canal in this part being somewhat differently arranged from those of the adjacent cuticle.

The sudoriparous glands are abundantly distributed over the whole surface of the body; but are especially numerous, as well as very large, in the skin of the palm of the hand, where, according to Krause, they amount to 2736 in each superficial square inch, and according to Mr. Erasmus Wilson, to as many as 3528. They are almost equally abundant and large in the skin of the sole. The glands by which the peculiar odorous matter of the axillæ is secreted form a nearly complete layer under the cutis, and are like the ordinary sudoriparous glands, except in being larger and having very short ducts. In the neck and back, where they are least numerous, the glands amount to 417 on the square inch (Krause). Their total number Krause estimates at 2,381,248; and, supposing the orifice of each gland to present a surface of $\frac{1}{56}$th of a line in diameter (and regarding a line as equal to $\frac{1}{10}$th of an inch), he reckons that the whole of the glands would present an evaporating surface of about eight square inches.*

* The peculiar bitter yellow substance secreted by the skin of the external auditory passage is named *cerumen*, and the glands themselves

Sebaceous Glands.—Besides the perspiration, the skin secretes a peculiar fatty matter, and for this purpose is provided with another set of special organs, termed *sebaceous glands* (fig. 115), which, like the sudoriparous glands, are abundantly distributed over most parts of the body. They are most numerous in parts largely supplied with hair, as the scalp and face, and are thickly distributed about the entrances of the various passages into the body, as the anus, nose, lips, and external ear. They are entirely absent from the palmar surface of the hands and the plantar surfaces of the feet. They are minutely lobulated glands, composed of an aggregate of small vesicles or sacculi filled with opaque white substances, like soft ointment. Minute capillary vessels overspread them; and their ducts, which have a bearded appearance, as if formed of rows of shells, open either on the surface of the skin, close to a hair, or, which is more usual, directly into the follicle of the hair. In the latter case, there are generally two glands to each hair (fig. 115).

Fig. 115.*

Structure of Hair and Nails.

Hair.—A hair is produced by a peculiar growth and

ceruminous glands; but they do not much differ in structure from the ordinary sudoriparous glands.

* Fig. 115. Sebaceous and sudoriparous glands of the skin (after Gurlt):—1, the thin cuticle; 2, the cutis; 3, adipose tissue; 4, a hair, in its follicle (5); 6, Sebaceous gland, opening into the follicle of the hair by an efferent duct; 7, the sudoriparous gland.

modification of the epidermis. Externally it is covered by a layer of fine scales closely imbricated, or overlapping like the tiles of a house, but with the free edges turned upwards (fig. 116, A). It is called the *cuticle* of the hair. Beneath this is a much thicker layer of elongated horny cells, closely packed together so as to resemble a fibrous structure. This, very commonly, in the human subject, occupies the whole of the inside of the hair; but in some

Fig. 116.

cases there is left a small central space filled by a substance called the *medulla* or *pith*, composed of small collections of irregularly shaped cells, containing fat- and pigment-granules.

The follicle, in which the root of each hair is contained, (fig. 117) forms a tubular depression from the surface of the skin,—descending into the subcutaneous fat, generally to a greater depth than the sudoriparous glands, and at its deepest part enlarging in a bulbous form, and often curving from its previous rectilinear course. It is lined throughout by cells of epithelium, continuous with those of the epidermis, and its walls are formed of pellucid membrane, which commonly, in the follicles of the largest hairs, has the structure of vascular fibro-cellular tissue. At the bottom of the follicle is a small papilla, or projection of true skin, and it is by the production and out-

* Fig. 116. *A*, surface of a white hair, magnified 160 diameters. The wave lines mark the upper or free edges of the cortical scales. *B*, separated scales, magnified 350 diameters (after Kölliker).

growth of epidermal cells from the surface of this papilla that the hair is formed. The inner wall of the follicle is

Fig. 117.*

Fig. 118.†

* Fig. 117. Medium-sized hair in its follicle, magnified 50 diameters (from Kölliker). *a*, stem cut short; *b*, root; *c*, knob; *d*, hair cuticle; *e*, internal, and *f*, external root-sheath; *g*, *h*, dermic coat of follicle; *i*, papilla; *k*, *k*, ducts of sebaceous glands; *l*, corium; *m*, mucous layer of epidermis; *o*, upper limit of internal root-sheath (from Kölliker).

† Fig. 118. Magnified view of the root of a hair (after Kohlrausch). *a*, stem or shaft of hair cut across; *b*, inner, and *c*, outer layer of the epidermal lining of the hair-follicle, called also the inner and outer root-sheath; *d*, dermal or external coat of the hair-follicle, shown in part,

lined by epidermal cells continuous with those covering the general surface of the skin; as if indeed the follicle had been formed by a simple thrusting in of the surface of the integument (figs. 117, 118). This epidermal lining of the hair-follicle, or *root-sheath* of the hair, is composed of two layers, the inner one of which is so moulded on the imbricated scaly cuticle of the hair, that its inner surface becomes imbricated also, but of course in the opposite direction. When a hair is pulled out, the inner layer of the *root-sheath* and part of the outer layer also are commonly pulled out with it.

Nails.—A *nail*, like a hair, is a peculiar arrangement of epidermal cells, the undermost of which, like those of the general surface of the integument, are rounded or elongated, while the superficial are flattened, and of more horny consistence. That specially modified portion of the corium, or true skin, by which the nail is secreted, is called the *matrix*.

The back edge of the nail, or the *root* as it is termed, is received into a shallow crescentic groove in the *matrix*, while the front part is free, and projects beyond the extremity of the digit. The intermediate portion of the nail rests by its broad under surface on the front part of the matrix, which is here called the *bed* of the nail. This part of the matrix is not uniformly smooth on the surface, but is raised in the form of longitudinal and nearly parallel ridges or laminæ, on which are moulded the epidermal cells of which the nail is made up (fig. 119).

The growth of the nail, like that of a hair, or of the epidermis generally, is effected by a constant production of cells from beneath and behind, to take the place of those which are worn or cut away. Inasmuch, however, as the

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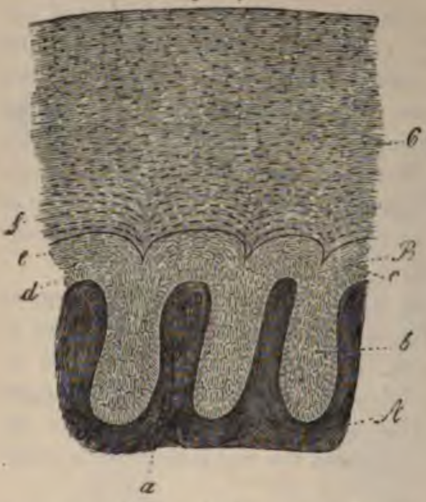
e, imbricated scales about to form a cortical layer on the surface of the hair. The adjacent cuticle of the root-sheath is not represented, and the papilla is hidden in the lower part of the knob where that is represented lighter.

posterior edge of the nail, from its being lodged in a groove of the skin, cannot grow backwards, on additions being made to it, so easily as it can pass in the opposite direction, any growth at its hinder part pushes the whole forwards. At the same time fresh cells are added to its under surface, and thus each portion of the nail becomes gradually thicker as it moves to the front, until, projecting beyond the surface of the matrix, it can receive no fresh addition from beneath, and is simply moved forwards by the growth at its root, to be at last worn away or cut off.

Fig. 119.*



Excretion by the Skin.

The skin, as already stated, is the seat of a two-fold excretion; of that formed by the sebaceous glands and hair-follicles, and of the more watery fluid, the *sweat* or *perspiration*, eliminated by the sudoriparous glands.

The secretion of the *sebaceous* glands and *hair-follicles*

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* Fig. 119. Vertical transverse section through a small portion of the nail and matrix largely magnified (after Kölliker).

A, corium of the nail-bed, raised into ridges or laminæ *a*, fitting in between corresponding laminæ *b*, of the nail. *B*, Malpighian, and *C*, horny layer of nail : *d*, deepest and vertical cells ; *e*, upper flattened cells of Malpighian layer.

(for their products cannot be separated) consists of cast-off epithelium-cells, with nuclei and granules, together with an oily matter, extractive matter, and stearin; in certain parts, also, it is mixed with a peculiar odorous principle, which is said by Dr. Fischer to contain caproic, butyric, and rutic acids. It is, perhaps, nearly similar in composition to the unctuous coating, or vernix caseosa, which is formed on the body of the fœtus while in the uterus, and which contains large quantities both of olein and margarin (J. Davy). Its purpose seems to be that of keeping the skin moist and supple, and, by its oily nature, of both hindering the evaporation from the surface, and guarding the skin from the effects of the long-continued action of moisture. But while it thus serves local purposes, its removal from the body entitles it to be reckoned among the excretions of the skin; though the share it has in the purifying of the blood cannot be discerned.

The fluid secreted by the *sudoriparous* glands is usually formed so gradually, that the watery portion of it escapes by evaporation as fast as it reaches the surface. But, during strong exercise, exposure to great external warmth, in some diseases, and when evaporation is prevented by the application of oiled silk or plaster, the secretion becomes more sensible and collects on the skin in the form of drops of fluid. A good analysis of the secretion of these glands, unmixed with other fluids secreted from the skin, can scarcely be made; for the quantity that can be collected pure is very small. Krause in a few drops from the palm of the hand, found an acid reaction, oily matter, and margarin, with water.

The *perspiration* of the skin, as the term is sometimes employed in physiology, includes all that portion of the secretions and exudations from the skin which passes off by evaporation; the *sweat* includes that which may be collected only in drops of fluid on the surface of the skin. The two terms are, however, most often used synonymously; and

for distinction, the former is called *insensible* perspiration: the latter, *sensible* perspiration. The fluids are the same, except that the sweat is commonly mingled with various substances lying on the surface of the skin. The contents of the sweat are, in part, matters capable of assuming the form of vapour, such as carbonic acid and water, and in part, other matters which are deposited on the skin, and mixed with the sebaceous secretion. Thenard collected the perspiration in a flannel shirt which had been washed in distilled water, and found in it chloride of sodium, acetic acid, some phospate of soda, traces of phosphate of lime, and oxide of iron, together with an animal substance. In sweat which had run from the forehead in drops, Berzelius found lactic acid, chloride of sodium, and chloride of ammonium. Anselmino placed his arm in a glass cylinder, and closed the opening around it with oiled silk, taking care that the arm touched the glass at no point. The cutaneous exhalation collected on the interior of the glass, and ran down as a fluid: on analysing this, he found water, acetate of ammonia, and carbonic acid; and in the ashes of the dried residue of sweat he found carbonate, sulphate, and phosphate of soda, and some potash, with chloride of sodium, phosphate and carbonate of lime, and traces of oxide of iron. Urea has also been shown to be an ordinary constituent of the fluid of perspiration.

The ordinary constituents of perspiration, may, therefore, according to Gorup-Besanez, be thus summed up: water, fat, acetic, butyric and formic acid, urea, and salts. The principal salts are the chlorides of sodium and potassium, together with, in small quantity, alkaline, and earthy phosphates and sulphates; and, lastly, some oxide of iron. Of these several substances, none, however, need particular consideration, except the carbonic acid and water.

The quantity of *watery vapour* excreted from the skin was estimated very carefully by Lavoisier and Sequin. The latter chemist enclosed his body in an air-tight bag,

with a mouth-piece. The bag being closed by a strong band above, and the mouth-piece adjusted and gummed to the skin around the mouth, he was weighed, and then remained quiet for several hours, after which time he was again weighed. The difference in the two weights indicated the amount of loss by pulmonary exhalation. Having taken off the air-tight dress, he was immediately weighed again, and a fourth time after a certain interval. The difference between the two weights last ascertained gave the amount of the cutaneous and pulmonary exhalation together; by subtracting from this the loss by pulmonary exhalation alone, while he was in the air-tight dress, he ascertained the amount of cutaneous transpiration. The repetition of these experiments during a long period, showed that, during a state of rest, the average loss by cutaneous and pulmonary exhalation in a minute, is from seventeen to eighteen grains,—the minimum eleven grains, the maximum thirty-two grains; and that of the eighteen grains, eleven pass off by the skin, and seven by the lungs. The maximum loss by exhalation, cutaneous and pulmonary, in twenty-four hours, is about $3\frac{3}{4}$ lb.; the minimum about $1\frac{1}{2}$ lb. Valentin found the whole quantity lost by exhalation from the cutaneous and respiratory surfaces of a healthy man who consumed daily 40,000 grains of food and drink, to be 19,000 grains, or $2\frac{5}{7}$ lb. Subtracting from this, for the pulmonary exhalation, 5,000 grains, and, for the excess of the weight of the exhaled carbonic acid over that of the equal volume of the inspired oxygen, 2,256 grains, the remainder, 11,744 grains, or nearly $1\frac{5}{7}$ lb., may represent an average amount of cutaneous exhalation in the day.

The large quantity of watery vapour thus exhaled from the skin, will prove that the amount excreted by simple transudation through the cuticle must be very large, if we may take Krause's estimate of about eight square inches for the total evaporating surface of the sudoriparous

glands; for not more than about 3,365 grains could be evaporated from such a surface in twenty-four hours, under the ordinary circumstances in which the surface of the skin is placed. This estimate is not an improbable one, for it agrees very closely with that of Milne-Edwards, who calculated that when the temperature of the atmosphere is not above 68° F., the glandular secretion of the skin contributes only $\frac{1}{6}$th to the total sum of cutaneous exhalation.

The quantity of watery vapour lost by transpiration, is of course influenced by all external circumstances which affect the exhalation from other evaporating surfaces, such as the temperature, the hygrometric state, and the stillness of the atmosphere. But, of the variations to which it is subject under the influence of these conditions, no calculation has been exactly made.

Neither, until recently, has there been any estimate of the quantity of *carbonic acid* exhaled by the skin on an average, or in various circumstances. Regnault and Reiset attempted to supply this defect, and concluded, from some careful experiments, that the quantity of carbonic acid exhaled from the skin of a warm-blooded animal is about $\frac{1}{50}$th of that furnished by the pulmonary respiration. Dr. Edward Smith's calculation is somewhat less than this. The cutaneous exhalation is most abundant in the lower classes of animals, more particularly the naked Amphibia, as frogs and toads, whose skin is thin and moist, and readily permits an interchange of gases between the blood circulating in it and the surrounding atmosphere. Bischoff found that, after the lungs of frogs had been tied and cut out, about a quarter of a cubic inch of carbonic acid gas was exhaled by the skin in eight hours. And this quantity is very large, when it is remembered that a full-sized frog will generate only about half a cubic inch of carbonic acid by his lungs and skin together in six hours (Milne-Edwards and Müller). That the respiratory func-

tion of the skin is, perhaps, even more considerable in the higher animals than appears to be the case from the experiments of Regnault and Reiset just alluded to, seemed probable by the fact observed by Magendie and others, that if the skin of animals is covered with an impermeable varnish, or the body enclosed, all but the head, in a caoutchouc dress, animals soon die, as if asphyxiated; their heart and lungs being gorged with blood, and their temperatures, during life, gradually falling many degrees, and sometimes as much as 36° F. below the ordinary standard (Magendie). Some recent experiments of Lashkewitzch appear, however, to confirm the opinion of Valentin, that loss of temperature is the immediate cause of death in these cases. A varnished animal is said to have suffered no harm when surrounded by cotton wadding, but it died when the wadding was removed.

Absorption by the skin has been already mentioned, as an instance in which that process is most actively accomplished. Metallic preparations rubbed into the skin have the same action as when given internally, only in a less degree. Mercury applied in this manner exerts its specific influence upon syphilis, and excites salivation; potassio-tartrate of antimony may excite vomiting, or an eruption extending over the whole body; and arsenic may produce poisonous effects. Vegetable matters, also, if soluble, or already in solution, give rise to their peculiar effects, as cathartics, narcotics, and the like, when rubbed into the skin. The effect of rubbing is probably to convey the particles of the matter into the orifices of the glands whence they are more readily absorbed than they would be through the epidermis. When simply left in contact with the skin, substances, unless in a fluid state, are seldom absorbed.

It has long been a contested question whether the skin covered with the epidermis has the power of absorbing water; and it is a point the more difficult to determine

because the skin loses water by evaporation. But, from the result of many experiments, it may now be regarded as a well-ascertained fact that such absorption really occurs. M.-Edwards has proved that the absorption of water by the surface of the body may take place in the lower animals very rapidly. Not only frogs, which have a thin skin, but lizards, in which the cuticle is thicker than in man, after having lost weight by being kept for some time in a dry atmosphere, were found to recover both their weight and plumpness very rapidly when immersed in water. When merely the tail, posterior extremities, and posterior part of the body of the lizard were immersed, the water absorbed was distributed throughout the system. And a like absorption through the skin, though to a less extent, may take place also in man.

Dr. Madden, having ascertained the loss of weight, by cutaneous and pulmonary transpiration, that occurred during half an hour in the air, entered the bath, and remained immersed during the same period of time, breathing through a tube which communicated with the air exterior to the room. He was then carefully dried and again weighed. Twelve experiments were performed in this manner; and in ten there was a gain of weight, varying from 2 scruples to 5 drachms and 4 scruples, or a mean gain of 1 drachm 2 scruples and 13 grains. The loss in the air during the same length of time (half an hour) varied in ten experiments from 2½ drachms to 1 ounce 2½ scruples, or in the mean was about 6½ drachms. So that, admitting the supposition that the cutaneous transpiration was entirely suspended, and estimating the loss by pulmonary exhalation at 3 drachms, there was, in these ten experiments of Dr. Madden, an average absorption of 4 drachms 1 scruple, and 3 grains, by the surface of the body, during half an hour. In four experiments performed by M. Berthold, the gain in weight was greater than in those of Dr. Madden.

In severe cases of dysphagia, when not even fluids can be taken into the stomach, immersion in a bath of warm water or of milk and water may assuage the thirst; and it has been found in such cases that the weight of the body is increased by the immersion. Sailors also, when destitute of fresh water, find their urgent thirst allayed by soaking their clothes in salt water and wearing them in that state; but these effects may be in part due to the hindrance to the evaporation of water from the skin.

The absorption, also, of different kinds of gas by the skin is proved by the experiments of Abernethy, Cruikshank, Beddoes, and others. In these cases, of course, the absorbed gases combine with the fluids, and lose the gaseous form. Several physiologists have observed an absorption of nitrogen by the skin. Beddoes says, that he saw the arm of a negro become pale for a short time when immersed in chlorine; and Abernethy observed that when he held his hands in oxygen, nitrogen, carbonic acid, and other gases contained in jars, over mercury, the volume of the gases became considerably diminished.

The share which the evaporation from the skin has in the maintenance of the uniform temperature of the body, and the necessary adaptation thereto of the production of heat, have been already mentioned (p. 239).

CHAPTER XV.

THE KIDNEYS AND THEIR SECRETION.

Structure of the Kidneys.

The kidney is covered on the outside by a rather tough fibrous capsule, which is slightly attached by its inner surface to the proper substance of the organ by means of very fine fibres of areolar tissue and minute blood-vessels. From the healthy kidney, therefore, it may be easily torn off without injury to the subjacent cortical portion of the organ. At the *hilus* or notch of the kidney, it becomes continuous with the external coat of the upper and dilated part of the ureter.

Fig. 120.*

On making a section length-wise through the kidney (fig. 120) the main part of its substance is seen to be composed of two chief portions, called respectively the *cortical* and the *medullary* portion, the latter being also some times called the *pyramidal* portion, from the fact of its being composed of about a

* Fig. 120. Plan of a longitudinal section through the pelvis and substance of the right kidney, ½; *a*, the cortical substance; *b*, *b*, broad part of the pyramids of Malpighi; *c*, *c*, the divisions of the pelvis named calyces, laid open; *c′*, one of these unopened; *d*, summit of the pyramids or papillæ projecting into calyces; *e*, *e*, section of the narrow part of two pyramids near the calyces; *p*, pelvis or enlarged divisions of the ureter within the kidney; *u*, the ureter; *s*, the sinus; *h*, the hilus.

dozen conical bundles of urine-tubes, each bundle being called a pyramid. The upper part of the duct of the organ, or the *ureter*, is dilated into what is called the *pelvis* of the kidney; and this, again, after separating into two or three principal divisions, is finally subdivided into still smaller portions, varying in number from about 8 to 12, or even more, and called *calyces*. Each of these little calyces or cups, again, receives the pointed extremity or *papilla* of a *pyramid*. Sometimes, however, more than one papilla is received by a *calyx*.

The kidney is a gland of the class called tubular, and both its cortical and medullary portions are composed essentially of secreting tubes, the *tubuli uriniferi*, which by one extremity, in the *cortical* portion, end commonly in little saccules containing blood-vessels, called *Malpighian bodies*, and by the other open through the *papillæ* into the pelvis of the kidney, and thus discharge the urine which flows through them.

Fig. 121.*

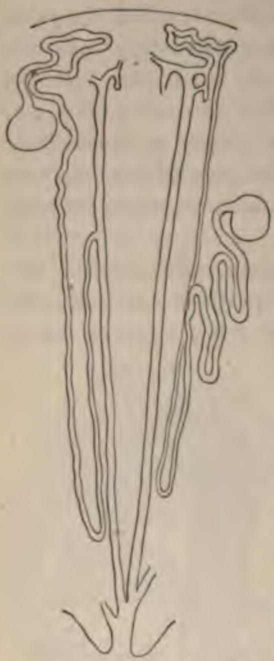
In the pyramids they are chiefly straight — dividing and diverging as they ascend through these into the cortical portion; while in the latter region they spread out more irregularly, and become much branched and convoluted.

The tubuli uriniferi (fig. 121) are composed of a nearly homogeneous membrane, lined internally by spheroidal epithelium, and for the greater part of their extent are about $\frac{1}{600}$ of an inch in diameter,—becoming somewhat

* Fig. 121. A. Portion of a secreting canal from the cortical substance of the kidney. B. The epithelium or gland-cells, more highly magnified (700 times).

larger than this immediately before they open through the *papillæ*. On tracing these tubules upwards from the papillæ, they are found to divide dichotomously as they ascend through the pyramids, and on reaching the bases of the latter, they begin to branch and diverge more widely, and to form by their branches and convolutions the essential part of the *cortical* portion of the organ. At their extremities they become dilated into the *Malpighian capsules.* Until recently, it was believed that the straight tubules in the pyramids branch out and become convoluted immediately on reaching the bases of the pyramids; but between the straight tubes in the pyramids and the convoluted tubes in the *cortical* portion, there has been shown to be a system of tubules of smaller diameter than either, which form intercommunications between the two varieties formerly recognised. These intervening tubules, called the *looped tubes of Henle,* arising from the straight tubes in

Fig. 122.*

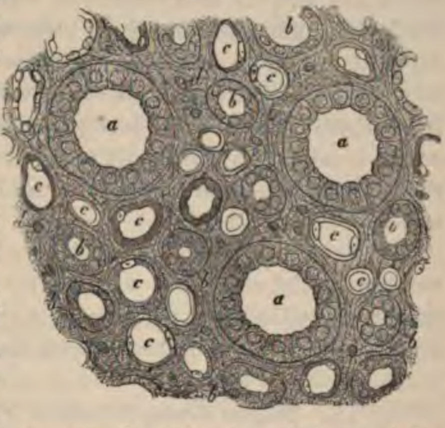


* Fig. 122. Diagram of the looped uriniferous tubes and their connection with the capsules of the glomeruli (from Southey, after Ludwig). In the lower part of the figure one of the large branching tubes is shown opening on a papilla; in the middle part two of the looped small tubes are seen descending to form their loops, and re-ascending in the medullary substance; while in the upper or cortical part, these tubes, after some enlargement, are represented as becoming convoluted and dilated in the capsules of glomeruli.

some part of their course, or being continued from their extremities at the bases of the pyramids, pass down loop-wise in the pyramids for a longer or shorter distance, and then, again turning up, end in the convoluted tubes whose extremities are dilated into the *Malpighian capsules* before referred to (fig. 122). On a transverse section of a pyramid (fig. 123), these looped tubes are seen to be of much smaller calibre than the straight ones, which are passing down to open through the papillæ.

The *Malpighian bodies* are found only in the cortical part of the kidney. On a section of the organ, some of them are just visible to the naked eye as minute red points; others are too small to be thus seen. Their average diameter is about $\frac{1}{120}$ of an inch. Each of them is composed of the dilated extremity of an urinary tube, or Malpighian *capsule*, enclosing a tuft of blood-vessels.

Fig. 123.*



In connection with these little bodies the general distribution of blood-vessels to the kidney may be here considered.

The renal artery divides into several branches, which, passing in at the hilus of the kidney, and covered by a fine sheath of areolar tissue derived from the capsule, enter the substance of the

* Fig. 123. Transverse section of a renal papilla (from Kölliker) $\frac{300}{1}$. *a*, larger tubes or papillary ducts; *b*, smaller tubes of Henle; *c*, blood-vessels, distinguished by their flatter epithelium; *d*, nuclei of the stroma.

organ chiefly in the intervals between the papillæ, and penetrate the cortical substance, where this dips down between the bases of the pyramids. Here they form a tolerably dense plexus of an arched form, and from this are given off smaller arteries which ultimately supply the Malpighian bodies.

Fig. 124.*

The small *afferent* artery (fig. 124), which enters the Malpighian body by perforating the *capsule*, breaks up in the interior into a dense and convoluted and looped capillary plexus, which is ultimately gathered up again into a single small *efferent* vessel, comparable to a minute vein, which leaves the Malpighian cupsule just by the point at which the afferent artery enters it. On leaving, it does not immediately join other small veins as might have been expected, but again breaking up into a network of capillary vessels, is distributed on the exterior of the tubule, from whose dilated end it had just emerged. After this second breaking up it is finally collected into a small vein, which, by union with others like it, helps to form the radicles of the renal vein.

The Malpighian *capsule* is lined by a layer of fine squamous epithelial cells; but whether the small glomerulus or tuft of capillaries in the interior is covered by a similar layer is uncertain. Kölliker believes that such a covering,

* Fig. 124. Diagram showing the relation of the Malpighian body to the uriniferous ducts and blood-vessels (after Bowman): *a*, one of the interlobular arteries; *a′*, afferent artery passing into the glomerulus; *c*, capsule of the Malpighian body, forming the termination of and continuous with *t*, the uriniferous tube; *e′*, *e′*, efferent vessels which subdivide in the plexus *p*, surrounding the tube, and finally terminate in the branch of the renal vein *e*.

although exceedingly thin, is present, and has delineated the appearance in the accompanying diagram (fig. 125).

Besides the small *afferent* arteries of the Malpighian bodies, there are, of course, others which are distributed in the ordinary manner, for nutrition's sake, to the different parts of the organ; and in the pyramids, between the tubes, there are numerous straight vessels, the *vasa recta*, supposed by some observers to be branches of *vasa efferentia* from Malpighian bodies, and therefore comparable to the venous plexus around the tubules in the *cortical* portion, while others think that they arise directly from small branches of the renal arteries.

Fig. 125.*

Between the tubes, vessels, etc., which make up the main substance of the kidney, there exists in small quantity a fine matrix of areolar tissue.

The nerves of the kidney are derived from the renal plexus.†

* Fig. 125. Semidiagrammatic representation of a Malpighian body in its relation to the uriniferous tube (from Kölliker) $\frac{300}{1}$. *a*, capsule of the Malpighian body; *d*, epithelium of the uriniferous tube; *e*, detached epithelium; *f*, afferent vessel; *g*, efferent vessel; *h*, convoluted vessels of the glomerulus.

† For a more detailed account of the structure of the kidney and a summary of the various opinions on the subject, the student may be referred especially to Quain's Anatomy, 7th ed., and to a paper by Dr. Reginald Southey in vol. i. of the St. Bartholomew's Hospital Reports.

Secretion of Urine.

The separation from the blood of the *solids* in a state of solution in the urine is probably effected, like other secretions, by the agency of the gland-cells, and equally in all parts of the urine-tubes. The urea and uric acid, and perhaps some of the other constituents existing ready formed in the blood, may need only separation, that is they may pass from the blood to the urine without further elaboration; but this is not the case with some of the other principles of the urine, such as the acid phosphates and the sulphates, for these salts do not exist as such in the blood, and must be formed by the chemical agency of the cells.

The *watery* part of the urine is probably in part separated by the same structures that secrete the solids, but the ingenious suggestion of Mr. Bowman that the water of the urine is mainly strained off, so to speak, by the Malpighian bodies, from the blood which circulates in their capillary tufts, is exceedingly probable; although if, as Kölliker and others maintain, there is an epithelial covering to these tufts or glomeruli, it is very likely that the solids of the urine may be in part secreted here also. We may, therefore, conclude that all parts of the tubular system of the kidney take part in the secretion of the urine as a whole, but that there is a provision also in the arrangement of the vessels in the Malpighian bodies for a more simple draining off of water from the blood when required.

The large size of the renal arteries and veins permits so rapid a transit of the blood through the kidneys, that the whole of the blood is purified by them. The secretion of urine is rapid in comparison with other secretions, and as each portion is secreted, it propels that which is already in the tubes onwards into the pelvis of the kidney. Thence through the ureter the urine passes into the bladder, into

which its rate and mode of entrance has been watched in cases of ectopia vesicæ, *i.e.*, of such fissures in the anterior and lower part of the walls of the abdomen, and of the front wall of the bladder, as exposed to view its hinder wall together with the orifices of the ureters. Some good observations on such cases were made by Mr. Erichsen. The urine does not enter the bladder at any regular rate, nor is there a synchronism in its movement through the two ureters. During fasting, two or three drops enter the bladder every minute, each drop as it enters first raising up the little papilla on which, in these cases, the ureter opens, and then passing slowly through its orifice, which at once again closes like a sphincter. In the recumbent posture, the urine collects for a little time in the ureters, then flows gently, and, if the body be raised, runs from them in a stream till they are empty. Its flow is increased in deep inspiration, or straining, and in active exercise, and in fifteen or twenty minutes after a meal.

The same observations, also, showed how fast some substances pass from the stomach through the circulation, and through the vessels of the kidneys. Ferrocyanide of potassium so passed on one occasion in a minute : vegetable substances, such as rhubarb, occupied from sixteen to thirty-five minutes; neutral alkaline salts with vegetable acids, which were generally decomposed *in transitu*, made the urine alkaline in from twenty-eight to forty-seven minutes. But the times of passage varied much; and the transit was always slow when the substances were taken during digestion.

The urine collecting in the urinary bladder is prevented from regurgitation into the ureters by the mode in which these pass through the walls of the bladder, namely, by their lying for between half and three-quarters of an inch between the muscular and mucous coats, and then turning rather abruptly forwards, and opening through the latter, it collects till the distension of the bladder is felt either by direct sensation, or, in ordinary cases, by a transferred

sensation at and near the orifice of the urethra. Then, the effort of the will being directed primarily to the muscles of the abdomen, and through them (by reason of its tendency to act with them) to the urinary bladder, the latter, though its muscular walls are really composed of involuntary muscle, contracts, and expels the urine. (See also p. 223).

The Urine: its general Properties.

Healthy urine is a clear limpid fluid, of a pale yellow or amber colour, with a peculiar faint aromatic odour, which becomes pungent and ammoniacal when decomposition takes place. The urine, though usually clear and transparent at first, often becomes as it cools opaque and turbid from the deposition of part of its constituents previously held in solution; and this may be consistent with health, though it is only in disease that, in the temperature of 98° or 100°, at which it is voided, the urine is turbid even when first expelled. Although ordinarily of pale amber colour, yet, consistently with health, the urine may be nearly colourless, or of a brownish or deep orange tint, and, between these extremes, it may present every shade of colour.

When secreted, and most commonly when first voided, the urine has a distinctly acid reaction in man and all carnivorous animals, and it thus remains till it is neutralized or made alkaline by the ammonia developed in it by decomposition. In most herbivorous animals, on the contrary, the urine is alkaline and turbid. The difference depends, not on any peculiarity in the mode of secretion, but on the differences in the food on which the two classes subsist: for when carnivorous animals, such as dogs, are restricted to a vegetable diet, their urine becomes pale, turbid, and alkaline, like that of an herbivorous animal, but resumes its former acidity on the return to an animal diet; while the urine voided by herbivorous animals, *e.g.*, rabbits, fed for some time exclusively upon animal sub-

stances, presents the acid reaction and other qualities of the urine of Carnivora, its ordinary alkalinity, being restored only on the substitution of a vegetable for the animal diet (Bernard). Human urine is not usually rendered alkaline by vegetable diet, but it becomes so after the free use of alkaline medicines, or of the alkaline salts with carbonic or vegetable acids; for these latter are changed into alkaline carbonates previous to elimination by the kidneys. Except in these cases, it is very rarely alkaline, unless ammonia has been developed in it by decomposition commencing before it is evacuated from the bladder.

The average *specific gravity* of the human urine is about 1020. Probably no other animal fluid presents so many varieties in density within twenty-four hours as the urine does; for the relative quantity of water and of solid constituents of which it is composed is materially influenced by the condition and occupation of the body during the time at which it is secreted, by the length of time which has elapsed since the last meal, and by several other accidental circumstances. The existence of these causes of difference in the composition of the urine has led to the secretion being described under the three heads of *urina sanguinis*, *urina potus*, and *urina cibi*. The first of these names signifies the urine, or that part of it which is secreted from the blood at times in which neither food nor drink has been recently taken, and is applied especially to the urine which is evacuated in the morning before breakfast. The *urina potus* indicates the urine secreted shortly after the introduction of any considerable quantity of fluid into the body: and the *urina cibi* the portions secreted during the period immediately succeeding a meal of solid food. The last kind contains a larger quantity of solid matter than either of the others; the first or second, being largely diluted with water, possesses a comparatively low specific gravity. Of these three kinds, the morning urine is the best calculated for analysis, since it represents the simple secretion unmixed with the elements

of food or drink; if it be not used, the whole of the urine passed during a period of twenty-four hours should be taken. In accordance with the various circumstances above-mentioned, the specific gravity of the urine may, consistently with health, range widely on both sides of the usual average. The average healthy range may be stated at from 1015 in the winter to 1025 in the summer, and variations of diet and exercise may make as great a difference. In disease, the variation may be greater; sometimes descending, in albuminuria, to 1004, and frequently ascending in diabetes, when the urine is loaded with sugar, to 1050, or even to 1060.

The whole *quantity* of urine secreted in twenty-four hours is subject to variation according to the amount of fluid drunk, and the proportion of the latter passing off from the skin, lungs, and alimentary canal. It is because the secretion of the skin is more active in summer than in winter, that the quantity of urine is smaller, and its specific gravity proportionately higher. On taking the mean of numerous observations by several experimenters, Dr. Parkes found that the average quantity voided in twenty-four hours by healthy male adults from twenty to forty years of age, amounted to 52½ fluid ounces.

Chemical Composition of the Urine.

The urine consists of water, holding in solution certain animal and saline matters as its ordinary constituents, and occasionally various matters taken into the stomach as food—salts, colouring matter, and the like. The quantities of the several natural and constant ingredients of the urine are stated somewhat differently by the different chemists who have analysed it; but many of the differences are not important, and the well-known accuracy of the several chemists renders it almost immaterial which of the analyses is adopted. The analysis by A. Becquerel being adopted by Dr. Prout, and by Dr. Golding Bird, will be here employed. (Table I.)

Table II. has been compiled from the observations of Dr. Parkes, and of numerous other authors quoted in his admirable work on the urine.

Table I.

Average quantity of each constituent of the Urine in 1000 parts.

Water			967·
Urea			14·230
Uric acid			·463
Colouring matter Mucus, and animal extractive mattter		inseparable from each other	10·167
Salts	Sulphates: Soda, Potash Bi-phosphates: Lime, Soda, Magnesia, Ammonia Chlorides: Sodium, Potassium Hippurate of soda Fluoride of potassium		8·135
Silica			traces
			1000·000

Table II.

Average quantity of the chief constituents of the Urine excreted in 24 hours by healthy male adults.

Water	52·	fluid ounces.
Urea	512·4	grains.
Uric acid	8·5	,,
Hippuric acid, uncertain,	probably 10 to 15·	,,
Sulphuric acid	31·11	,,
Phosphoric acid	45·	,,
Chlorine	105·0	,,
Chloride of Ammonium	35·25	,,
Potash	58·	,,
Soda	125·	,,
Lime	3·5	,,
Magnesia	3·	,,
Mucus	7·	,,
Extractives: Creatin, Creatinin, Pigment, Xanthin, Hypoxanthin, Resinous matter, *etc.*	154·0	,,

From these proportions, however, most of the constituents are, even in health, liable to variations. Especially the *water* is so. Its variations in different seasons, and according to the quantity of drink and exercise, have already been mentioned. It is also liable to be influenced by the condition of the nervous system, being sometimes greatly increased in hysteria, and some other nervous affections; and at other times diminished. In some diseases it is enormously increased; and its increase may be either attended with an augmented quantity of solid matter, as in ordinary diabetes, or may be nearly the sole change, as in the affection termed diabetes insipidus. In other diseases, *e.g.*, the various forms of albuminuria, the quantity may be considerably diminished. A febrile condition almost always diminishes the quantity of water; and a like diminution is caused by any affection which draws off a large quantity of fluid from the body through any other channel than that of the kidneys, *e.g.*, the bowels and the skin.

Fig. 126.*

Urea.—Urea is the principal solid constituent of the urine, forming nearly one-half of the whole quantity of solid matter. It is also the most important ingredient, since it is the chief substance by which the nitrogen of decomposed tissue and superfluous food is excreted from the body. For its removal, the secretion of urine seems especially provided; and by its retention in the blood the most pernicious effects are produced.

Urea, like the other solid constituents of the urine,

* Fig. 126. Crystals of urea.

exists in a state of solution. But it may be procured in the solid state, and then appears in the form of delicate silvery acicular crystals, which, under the microscope, appear as four-sided prisms (fig. 126). It is obtained in this state by evaporating urine carefully to the consistence of honey, acting on the inspissated mass with four parts of alcohol, then evaporating the alcoholic solution, and purifying the residue by repeated solution in water or alcohol, and finally allowing it to crystallise. It readily combines with an acid, like a weak base; and may thus be conveniently procured in the form of a nitrate, by adding about half a drachm of pure nitric acid to double that quantity of urine in a watch glass. The crystals of nitrate of urea are formed more rapidly if the urine have been previously concentrated by evaporation.

Urea is colourless when pure; when impure, yellow or brown: without smell, and of a cooling, nitre-like taste; has neither an acid nor an alkaline re-action, and deliquesces in a moist and warm atmosphere. At 59° F. it requires for its solution less than its weight of water; it is dissolved in all proportions by boiling water; but it requires five times its weight of cold alcohol for its solution. At 248° F. it melts without undergoing decomposition; at a still higher temperature ebullition takes place, and carbonate of ammonia sublimes; the melting mass gradually acquires a pulpy consistence; and, if the heat is carefully regulated, leaves a grey-white powder, cyanic acid.

Urea is identical in composition with cyanate of ammonia, and was first artificially produced by Wohler from this substance. Thus:—

$$\underset{\text{Cyanate of Ammonia.}}{CHNO.\ H_3N} = \underset{\text{Urea.}}{CH_4N_2O.}$$

The action of heat upon urea in evolving carbonate of ammonia, and leaving cyanic acid, is thus explained. A similar decomposition of the urea with development of carbonate of ammonia ensues spontaneously when urine is

kept for some days after being voided, and explains the ammoniacal odour then evolved. It is probable, that this spontaneous decomposition is accelerated by the mucus and other animal matters in the urine, which, by becoming putrid, act the part of a ferment and excite a change of composition in the surrounding compounds. It is chiefly thus that the urea is sometimes decomposed before it leaves the bladder, when the mucous membrane is diseased, and the mucus secreted by it is both more abundant and, probably, more prone than usual to become putrid. The same occurs also in some affections of the nervous system, particularly in paraplegia.

The quantity of urea excreted is, like that of the urine itself, subject to considerable variation. It is materially influenced by diet, being greater when animal food is exclusively used, less when the diet is mixed, and least of all with a vegetable diet. As a rule, men excrete a larger quantity than women, and persons in the middle periods of life a larger quantity than infants or old people (Lecanu). The quantity of urea does not necessarily increase and decrease with that of the urine, though on the whole it would seem that whenever the amount of urine is much augmented, the quantity of urea also is usually increased (Becquerel); and it appears from observations of Genth, that the quantity of urea, as of urine, may be especially increased by drinking large quantities of water. In various diseases, as albuminuria, the quantity is reduced considerably below the healthy standard, while in other affections it is above it.

The urea appears to be derived from two different sources. That it is derived in part from the unassimilated elements of nitrogenous food, circulating with the blood, is shown in the increase which ensues on substituting an animal or highly nitrogenous for a vegetable diet; in the much larger amount, nearly double, excreted by Carnivora than Herbivora, independent of exercise; and in its diminution to

about one-half during starvation, or during the exclusion of non-nitrogenous principles of food. But that it is in larger part derived from the disintegration of the azotized animal tissues, is shown by the fact that it continues to be excreted, though in smaller quantity than usual, when all nitrogenous substances are strictly excluded from the food, as when the diet consists for several days of sugar, starch, gum, oil, and similar non-azotized vegetable substances (Lehmann). It is excreted also, even though no food at all be taken for a considerable time; thus it is found in the urine of reptiles which have fasted for months; and in the urine of a madman, who had fasted eighteen days, Lassaigne found both urea and all the components of healthy urine. Probably all the nitrogenous tissues furnish a share of urea by their decomposition.

It has been commonly taken for granted that the quantity of urea in the urine is greatly increased by active exercise; but numerous observers have failed to detect more than a slight increase under such circumstances; and our notions concerning the relation of this excretory product to the destruction of muscular fibre, consequent on the exercise of the latter, have lately undergone considerable modification. There is no doubt, of course, that like all parts of the body, the muscles have but a limited term of existence, and are being constantly renewed, at the same time that a part of the products of their disintegration appears in the urine in the form of urea. But the waste is not so fast as it has been frequently supposed to be; and the theory that the amount of work done by the muscle is expressed by the quantity of urea excreted in the urine, and that each act of contraction corresponds to an *equivalent* waste of muscle-structure, is founded on error. (See also chapter on Motion.)

Urea exists ready-formed in the blood, and is simply abstracted therefrom by the kidneys. It may be detected in small quantity in the blood, and in some other parts of

the body, *e.g.*, the humours of the eye (Millon), even while the functions of the kidneys are unimpaired: but when from any cause, especially extensive disease or extirpation of the kidneys, the separation of urine is imperfect, the urea is found largely in the blood and in most other fluids of the body.

Uric Acid.—This, which is another nitrogenous animal substance, with the formula $C_5N_4H_4O_3$, and was formerly termed lithic acid, on account of its existence in many forms of urinary calculi, is rarely absent from the urine of man or animals, though in the feline tribe it seems to be sometimes entirely replaced by urea (G. Bird). Its proportionate quantity varies considerably in different animals. In man, and Mammalia generally, especially the Herbivora, it is comparatively small. In the whole tribe of birds and of serpents, on the other hand, the quantity is very large, greatly exceeding that of the urea. In the urine of granivorous birds, indeed, urea is rarely if ever found, its place being entirely supplied by uric acid. The quantity of uric acid, like that of urea, in human urine, is increased by the use of animal food, and decreased by the use of food free from nitrogen, or by an exclusively vegetable diet. In most febrile diseases, and in plethora, it is formed in unnaturally large quantities; and in gout it is deposited in, and in the tissues around, joints, in the form of urate of soda, of which the so-called chalk-stones of this disease are principally composed.

Fig. 127.*

* Fig. 127. Various forms of uric acid crystals.

The condition in which uric acid exists in solution in the urine has formed the subject of some discussion, because of its difficult solubility in water.

According to Liebig the uric acid exists as urate of soda, produced, he supposes, by the uric acid, as soon as it is formed, combining with part of the base of the alkaline phosphate of soda of the blood. Hippuric acid, which exists in human urine also, he believes, acts upon the alkaline phosphate in the same way, and increases still more the quantity of acid phosphate, on the presence of which it is probable that a part of the natural acidity of the urine depends. It is scarcely possible to say whether the union of uric acid with the base soda and probably ammonia, takes place in the blood, or in the act of secretion in the kidney: the latter is the more probable opinion; but the quantity of either uric acid or urates in the blood is probably too small to allow of this question being solved.

The source of uric acid is probably in the disintegrated elements of albuminous tissues. The relation which uric acid and urea bear to each other is, however, still obscure. The fact that they often exist together in the same urine, makes it seem probable that they have different origins or different offices to perform; but the entire replacement of either by the other, as of urea by uric acid in the urine of birds, serpents, and many insects, and of uric acid by urea, in the urine of the feline tribe of Mammalia, shows that each alone may discharge all the important functions of the two.

Owing to its existence in combination in healthy urine, uric acid for examination must generally be precipitated from its bases by a stronger acid. Frequently, however, when excreted in excess, it is deposited in a crystalline form (fig. 127), mixed with large quantities of urate of ammonia or soda (fig. 130). In such cases it may be procured for microscopic examination, by gently warming

the portion of urine containing the sediment; this dissolves urate of ammonia and soda, while the comparatively insoluble crystals of uric acid subside to the bottom.

The most common form in which uric acid is deposited in urine, is that of a brownish or yellowish powdery substance, consisting of granules of urate of ammonia or soda. When deposited in crystals, it is most frequently in rhombic or diamond-shaped laminæ, but other forms are not uncommon (fig. 127). When deposited from urine, the crystals are generally more or less deeply coloured, by being combined with the colouring principles of the urine.

Fig. 128.*

Hippuric Acid has long been known to exist in the urine of herbivorous animals in combination with soda. Liebig has shown that it also exists naturally in the urine of man, in quantity equal to the uric acid, and Weismann's observations agree with this. It is a nitrogenous compound with the formula $C_9H_9NO_3$. It is closely allied to benzoic acid; and this substance when introduced into the system, is excreted by the kidneys as hippuric acid (Ure). Its source is not satisfactorily determined: in part it is probably derived from some constituents of vegetable diet, though man has no hippuric acid in his food, nor, commonly, any benzoic acid that might be converted into it; in part from the natural disintegration of tissues, independent of vegetable food, for Weismann constantly found an appreciable quantity, even when living on an exclusively animal diet.

* Fig. 128. Crystals of hippuric acid.

The nature and composition of the *colouring matter* of urine are involved in some obscurity. It is probably closely related to the colouring matter of the blood.

Fig. 129.*

The *mucus* in the urine consists principally of the epithelial débris of the mucous surface of the urinary passages. Particles of epithelium, in greater or less abundance, may be detected in most samples of urine, especially if it has remained at rest for some time, and the lower strata are then examined (fig. 129). As urine cools, the mucus is sometimes seen suspended in it as a delicate opaque cloud, but generally it falls. In inflammatory affections of the urinary passages, especially of the bladder, mucus in large quantities is poured forth, and speedily undergoes decomposition. The presence of the decomposing mucus excites (as already stated) chemical changes in the urea, whereby ammonia, or carbonate of ammonia, is formed, which, combining with the excess of acid in the superphosphates in the urine, produces insoluble neutral or alkaline phosphates of lime and magnesia, and phosphate of ammonia and magnesia. These, mixing with the mucus, constitute the peculiar white, viscid, mortar-like substance which collects upon the mucous surface of the bladder, and is often passed with the urine, forming a thick, tenacious sediment.

Besides mucus and colouring matter, urine contains a considerable quantity of animal matter, usually described under the obscure name of *animal extractive*. The investigations of Liebig, Heintz, and others, have shown that

* Fig. 129. Mucus deposited from urine.

some of this ill-defined substance consists of *Creatin* and *Creatinin*, two crystallizable substances derived, probably, from the metamorphosis of muscular tissue. These substances appear to be intermediate between the proper elements of the muscles, and, perhaps, of other azotized tissues and urea: the first products of the disintegrating tissues probably consisting not of urea, but of Creatin and Creatinin, which subsequently are partly resolved into urea, partly discharged, without change, in the urine. The names of some other substances of which there are commonly traces in the urine, will be found in Table II., p. 451. It has been shown by Scherer that much of the substance classed as extractive matter of the urine, is the peculiar colouring matter, probably derived from the hæmo-globin of the blood.

Saline Matter.—The sulphuric acid in the urine is combined chiefly or entirely with soda and potash: forming salts which are taken in very small quantity with the food, and are scarcely found in other fluids or tissues of the body; for the sulphates commonly enumerated among the constituents of the ashes of the tissues and fluids are, for the most part or entirely, produced by the changes that take place in the burning. Dr. Parkes, indeed, considers that only about one-third of the sulphuric acid found in the urine is derived directly from the food. Hence the greater part of the sulphuric acid which the sulphates in the urine contain, must be formed in the blood, or in the act of secretion of urine; the sulphur of which the acid is formed, being probably derived from the decomposing nitrogenous tissues, the other elements of which are resolved into urea and uric acid. It may be in part derived also, as Dr. Parkes observes, from the sulphur-holding taurin and cystin which can be found in the liver, lungs, and other parts of the body, but not generally in the excretions; and which, therefore, must be broken up. The oxygen is supplied through the lungs, and the heat gene-

rated during combination with the sulphur, is one of the subordinate means by which the animal temperature is maintained.

Besides the sulphur in these salts, some also appears to be in the urine, uncombined with oxygen; for after all the sulphates have been removed from urine, sulphuric acid may be formed by drying and burning it with nitre. Mr. Ronalds believes that from three to five grains of sulphur are thus daily excreted. The combination in which it exists is certain: possibly it is in some compound analogous to cystin or cystic oxide (p. 462).

The *phosphoric acid* in the urine is combined partly with the alkalies, partly with the alkaline earths—about four or five times as much with the former as with the latter. In blood, saliva, and other alkaline fluids of the body, phosphates exist in the form of alkaline, or neutral acid salts. In the urine they are acid salts, viz., the phosphates of sodium, ammonium, calcium and magnesium, the excess of acid being, according to Liebig, due to the appropriation of the alkali with which the phosphoric acid in the blood is combined, by the several new acids which are formed or discharged at the kidneys, namely, the uric, hippuric, and sulphuric acids, all of which he supposes to be neutralized with soda.

The presence of the acid phosphates accounts, in great measure, or, according to Liebig, entirely, for the acidity of the urine. The phosphates are taken largely in both vegetable and animal food; some thus taken, are excreted at once; others, after being transformed and incorporated with the tissues. Phosphate of calcium forms the principal earthy constituent of bone, and from the decomposition of the osseous tissue the urine derives a large quantity of this salt. The decomposition of other tissues also, but especially of the brain and nerve-substance, furnishes large supplies of phosphorus to the urine, which phosphorus is supposed, like the sulphur, to be united with oxygen, and

then combined with bases. This quantity is, however, liable to considerable variation. Any undue exercise of the mind, and all circumstances producing nervous exhaustion, increase it. The earthy phosphates are more abundant after meals, whether on animal or vegetable food, and are diminished after long fasting. The alkaline phosphates are increased after animal food, diminished after vegetable food. Exercise increases the alkaline, but not the earthy phosphates (Bence Jones). Phosphorus uncombined with oxygen appears, like sulphur, to be excreted in the urine (Ronalds). When the urine undergoes alkaline fermentation, phosphates are deposited in the form of an *urinary sediment* consisting chiefly of phosphate of ammonia and magnesia (triple phosphate) (fig. 130). This compound does not, as such, exist in healthy urine. The ammonia is chiefly or wholly derived from the decomposition of urea (p. 453).

Fig. 130.*

The chlorine of the urine occurs chiefly in combination with sodium, but slightly also with ammonium, and, perhaps, potassium. As the chlorides exist largely in food, and in most of the animal fluids, their occurrence in the urine is easily understood.

Cystin (fig. 132) is an occasional constituent of urine. It resembles taurin in containing a large quantity of sulphur—more than 25 per cent. It does not exist in healthy urine.

Another common morbid constituent of the urine is

* Fig. 130. Urinary sediment of triple phosphates (large prismatic crystals) and urate of ammonia, from urine which had undergone alkaline fermentation.

oxalic acid, which is frequently deposited in combination

Fig. 131.*

Fig. 132.†

with lime (fig. 131) as an urinary sediment. Like cystin, but much more commonly, it is the chief constituent of certain calculi.

A small quantity of gas is naturally present in the urine in a state of solution. It consists chiefly of carbonic acid and nitrogen.

CHAPTER XVI.

THE NERVOUS SYSTEM.

The nervous system consists of two portions or systems, the *cerebro-spinal* and the *sympathetic* or *ganglionic*, each of which (though they have many things in common) possesses certain peculiarities in structure, mode of action, and range of influence.

The *cerebro-spinal* system includes the brain and spinal cord, with the nerves proceeding from them, and the several ganglia seated upon these nerves, or forming part of the

* Fig. 131. Crystals of oxalate of lime.
† Fig. 132. Crystals of cystin.

substance of the brain. It was denominated by Bichât the nervous system of *animal* life; and includes all the nervous organs in and through which are performed the several functions with which the mind is more immediately connected, namely, those relating to sensation and volition, and the mental acts connected with sensible things.

The *sympathetic* or *ganglionic* portion of the nervous system, which Bichât named the nervous system of *organic** life, consists essentially of a chain of ganglia connected by nervous cords, which extend from the cranium to the pelvis, along each side of the vertebral column, and from which, nerves with ganglia proceed to the viscera in the thoracic, abdominal, and pelvic cavities. By its distribution, as well as by its peculiar mode of action, this system is less immediately connected with the mind, either as conducting sensations or the impulses of the will; it is more closely connected than the cerebro-spinal system is with the processes of organic life.

The differences however, between these two systems, are not essential: their actions differ in degree and object more than in kind or mode.

Elementary Structures of the Nervous System.

The organs of the nervous system or systems are composed essentially of two kinds of structure, vesicular and fibrous; both of which appear essential to the construction of even the simplest nervous system. The vesicular

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* The term *organic* is often used in connection with a function, such as digestion or secretion, which belongs to all organised beings alike; while the term *animal* function, or *animal* life, is used in connection with such qualities as volition or motion, which seem altogether or in great part to belong only to animals. The terms which have been thus used in this general way, are often loosely applied to special tissues. Thus *organic* nerve-fibres are those which are distributed especially to organs concerned in the discharge of the functions of *organic*, as distinguished from *animal* life; and the term is still more commonly applied to one kind of muscular fibre.

structure is usually collected in masses, and mingled with the fibrous structure, as in the brain, spinal cord, and the several ganglia; and these masses constitute what are termed *nerve-centres*, being the organs in which it is supposed that nervous force may be generated, and in which are accomplished all the various reflections and other modes of disposing of impressions when they are not simply conducted along nerve-fibres. The fibrous nerve-substance, besides entering into the composition of the nervous centres, forms alone the *nerves*, or cords of communication, which connect the various nervous centres, and are distributed in the several parts of the body, for the purpose of conveying nervous force to them, or of transmitting to the nervous centres the impressions made by stimuli.

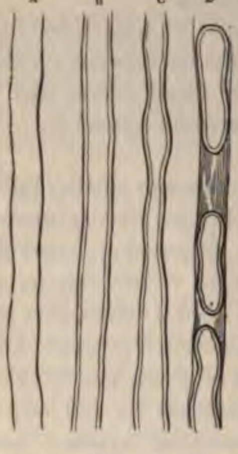
Along the nerve-fibres impressions or conditions of excitement are simply conducted: in the nervous centres they may be made to deviate from their direct course, and be variously diffused, reflected, or otherwise disposed of.

Nerves are constructed of minute fibres or tubules full of nervous matter, arranged in parallel or interlacing bundles, which bundles are connected by intervening connective tissue, in which their principal blood-vessels ramify. A layer of the areolar, or of strong fibrous tissue, also surrounds the whole nerve, and forms a sheath or neurilemma for it. In most nerves, two kinds of fibres are mingled; those of one kind being most numerous in, and characteristic of, nerves of the cerebro-spinal system; those of the other, most numerous in nerves of the sympathetic system.

The fibres of the first kind appear to consist of tubules of a pellucid simple membrane, within which is contained the proper nerve substance, consisting of transparent oil-like, and apparently homogeneous material, which gives to each fibre the appearance of a fine glass tube filled with a clear transparent fluid (fig. 133, A). This simplicity of

composition is, however, only apparent in the fibres of a perfectly fresh nerve; for, shortly after death, they undergo changes which make it probable that their contents are composed of two different materials. The internal or central part, occupying the axis of the tube, becomes greyish, while the outer, or cortical portion, becomes opaque and dimly granular or grumous, as if from a kind of coagulation. At the same time, the fine outline of the previously transparent cylindrical tube is exchanged for a dark double contour (fig. 133, B), the outer line being formed by the sheath of the fibre, the inner by the margin of curdled or coagulated medullary substance. The granular material shortly collects into little masses, which distend portions of the tubular membrane, while the intermediate spaces collapse, giving the fibres a varicose, or beaded appearance (fig. 133 C and D), instead of the previous cylindrical form.

Fig. 133.*



The difference produced in the contents of the nerve-fibres when exposed to the same conditions, has, with other facts, led to the opinion now generally adopted, that the central part or *axis-cylinder* of each nerve-fibre differs from the outer portion. The outer portion is usually called the medullary or *white*

* Fig. 133. Primitive nerve-tubules. A. A perfectly fresh tubule with a single dark outline. B. A tubule or fibre with a double contour from commencing post-mortem change. C. The changes further advanced, producing a varicose or beaded appearance. D. A tubule or fibre, the central part of which, in consequence of still further changes, has accumulated in separate portions within the sheath (after Wagner).

substance of Schwann, being that to which the peculiar white aspect of cerebro-spinal nerves is principally due. The whole contents of the nerve-tubules appear to be extremely soft, for when subjected to pressure they readily pass from one part of the tubular sheath to another, and often cause a bulging at the side of the membrane. They also readily escape, on pressure, from the extremities of the tubule, in the form of a grumous or granular material.

That there is an essential difference in chemical composition between the central and circumferential parts of the nerve-fibre, *i.e.*, between the axis-cylinder and the medullary sheath, has of late been clearly shown by Messrs. Lister and Turner. Their observations, founded on Mr. Lockhart Clarke's method of investigating nervous substance by means of chromic acid and carmine, have shown that the axis-cylinder of the nerve-fibre is unaffected by chromic acid, but imbibes carmine with great facility, while the medullary sheath is rendered opaque and brown and laminated by chromic acid, but is entirely untinged by the carmine. From this difference in their chemical behaviour, the central and circumferential portions of the nerve-fibres are readily distinguished on microscopic examination, the former being indicated by a bright red carmine-coloured point, the latter by a pale ring surrounding it. The laminated character of the medullary sheath after treatment with chromic acid is believed by Mr. Lockhart Clarke to be due to corrugations effected by the acid, and not to its having a fibrous structure, as maintained by Stilling.

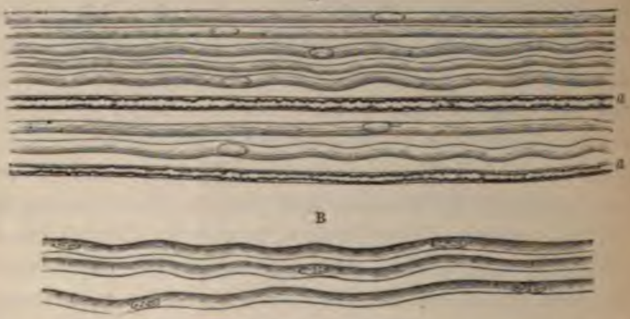
The size of the nerve-fibres varies, and the same fibres do not preserve the same diameter through their whole length, being largest in their course within the trunks and branches of the nerves, in which the majority measure from $\frac{1}{2000}$ to $\frac{1}{3000}$ of an inch in diameter. As they approach the brain or spinal cord, and generally also in

the tissues in which they are distributed, they gradually become smaller. In the grey or vesicular substance of the brain or spinal cord, they generally do not measure more than from $\frac{1}{10000}$ to $\frac{1}{14000}$ of an inch.

The fibres of the second kind (fig. 134), which constitute the whole of the branches of the olfactory nerves, the principal part of the trunk and branches of the sympathetic nerves, and are mingled in various proportions in the cerebro-spinal nerves, differ from the preceding, chiefly in their fineness, being only about $\frac{1}{2}$ or $\frac{1}{3}$ as large in their course within the trunks and branches of the nerves; in

Fig. 134.*

A



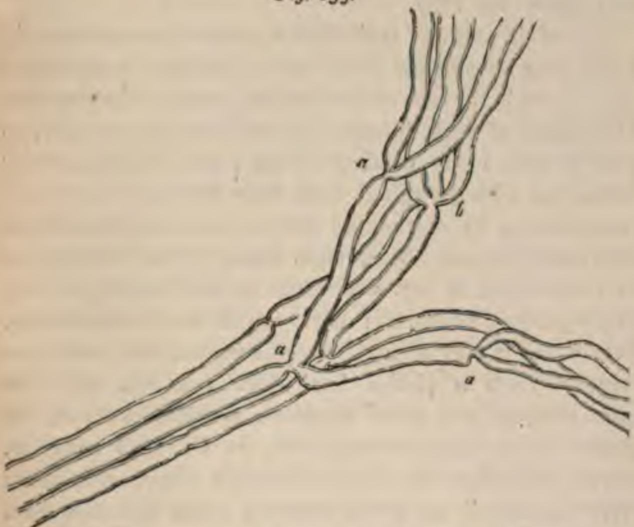
the absence of the double contour; in their contents being apparently uniform; and in their having, when in bundles, a yellowish-grey hue instead of the whiteness of the cerebro-spinal nerves. These peculiarities make it probable that they differ from the other nerve-fibres in not possessing the outer layer of white or medullary nerve-substance; and that their contents are composed exclusively

* Fig. 134. Grey, pale, or gelatinous nerve-fibres (from Max Schultze), magnified between 400 and 500 diameters. A. from branch of the olfactory nerve of the sheep; *a*, *a*, two dark-bordered or white fibres from the fifth pair, associated with the pale olfactory fibres. B. From the sympathetic nerve.

of the substance corresponding with the central portion, or axis-cylinder of the larger fibres. Yet since many nerve-fibres may be found which appear intermediate in character between these two kinds, and since the large fibres, as they approach both their central and their peripheral end, gradually diminish in size, and assume many of the other characters of the fine fibres of the sympathetic system, it is not necessary to suppose that there must be a material difference in the office or mode of action of the two kinds of fibres.

Every nerve-fibre in its course proceeds uninterruptedly from its origin at a nervous centre to near its destination,

Fig. 135.*



whether this be the periphery of the body, another nervous centre, or the same centre whence it issued.

* Fig. 135. Small branch of a muscular nerve of the frog, near its termination, showing divisions of the fibres. *a*, into two; *b*, into three; magnified 350 diameters (from Kölliker).

Bundles, or fasciculi of fibres, run together in the nerves, but merely lie in apposition with each other; they do not unite: even when the fasciculi anastomose, there is no *union* of fibres, but only an *interchange* of fibres between the anastomosing fasciculi. Although each nerve-fibre is thus single and undivided through nearly its whole course, yet as it approaches the region in which it terminates, individual fibres break up into several subdivisions (fig. 135) before their final ending in the different fashions to be immediately described. The white or *medullated* nerve-fibres (fig. 133), moreover, lose their medullary sheath or white substance of Schwann before their final distribution, and acquire the characters more or less of the pale or grey fibres (fig. 134).

At certain parts of their course, nerves form *plexuses*, in which they anastomose with each other, and interchange fasciculi, as in the case of the brachial and lumbar plexuses. The object of such interchange of fibres is, probably, to give to each nerve passing off from the plexus, a wider connection with the spinal cord than it would have if it proceeded to its destination without such communication with other nerves. Thus, each nerve by the wideness of its connections, is less dependent on the integrity of any single portion, whether of nerve-centre or of nerve-trunk, from which it may spring. By this means, also, each part supplied from a plexus has wider relations with the nerve-centres, and more extensive sympathies; and, by means of the same arrangement, as Dr. Gull suggests, groups of muscles may be associated for combined actions; every member of the group receiving motor filaments from the same parts of the nerve-centre.

The *terminations* of nerve-fibres are their modes of distribution and connection in the nerve-centres, and in the parts which they supply: the former are called their *central*, the latter their *peripheral* terminations.

The *peripheral* termination of nerve-fibres has been always the subject of considerable discussion and doubt. The following appear to be the chief modes of ending of nerve-fibres in the parts they supply:—

1. In fine networks or plexuses; examples of this are found in the distribution of nerves in muscles, and in mucous and serous membranes. 2. In special terminal organs, called *touch-corpuscles* (fig. 113), *end-bulbs* (fig. 114), and *Pacinian bodies* (figs. 136, 137). 3. In cells; as in the eye and internal ear, and some other parts. 4. In free ends; as from the fine plexuses in muscles, according to Kolliker. 5. In muscles, a peculiar termination of nerves in small bodies called *motorial end-plates*, has been described by Rouget and others. These small bodies, varying from $\frac{1}{5000}$ to $\frac{1}{350}$ of an inch in diameter, and placed by different observers outside and inside the sarcolemma, are fixed to the muscular fibres, one for each, and to them the extremity of a minute branch of nerve-fibre is attached. These little plates appear to be formed of an expansion of the end of a nerve-fibre with a small quantity of connective tissue.

The Pacinian bodies or corpuscles (figs. 136 and 137), to which reference has been just made, are little elongated oval bodies, situated on some of the cerebro-spinal and sympathetic nerves, especially the cutaneous nerves of the hands and feet; and on branches of the large sympathetic plexus about the abdominal aorta (Kölliker). They often occur also on the nerves of the mesentery, and are especially well seen in the mesentery of the cat. They are named Pacinian, after their discoverer Pacini. Each corpuscle is attached by a narrow pedicle to the nerve on which it is situated; it is formed of several concentric layers of fine membrane, with intervening spaces containing fluid; through its pedicle passes a single nerve-fibre, which, after traversing the several concentric layers and their immediate spaces, enters a central cavity, and, gradually

losing its dark border, and becoming smaller, terminates at or near the distal end of the cavity, in a knob-like enlargement, or in a bifurcation. The enlargement commonly found at the end of the fibre, is said by Pacini to resemble a ganglion-corpuscle; but this observation has

Fig. 136.*

Fig. 137.†

not been confirmed. The physiological import of these bodies seems to be still quite obscure.

The *central* termination of nerve-fibres can be better considered after the account of the vesicular nerve-substance.

* Fig. 136. Extremities of a nerve of the finger with Pacinian corpuscles attached, about the natural size (adapted from Henle and Kölliker).

† Fig. 137. A magnified view of a single Pacinian corpuscle, showing its laminated structure, and the termination of the nerve-fibre in its central cavity (after Bendz).

The *vesicular* nervous substance contains, as its name implies, *vesicles* or *corpuscles*, in addition to fibres; and a structure, thus composed of corpuscles and inter-communicating fibres, usually constitutes a *nerve-centre:* the chief nerve-centres being the grey matter of the brain and spinal cord, and the various so-called *ganglia*. In the brain and spinal cord a fine stroma of retiform tissue called the *neuroglia* extends throughout both the fibrous

Fig. 138.*

Fig. 139.†

and vesicular nervous substance, and forms a supporting and investing frame-work for the whole.

The *nerve-corpuscles*, which give to the ganglia and to certain parts of the brain and spinal cord the peculiar greyish or reddish-grey aspect by which these parts are characterized, are large, nucleated cells, filled with a finely granular material, some of which is often dark like pig-

* Fig. 138. Nerve-corpuscles from a ganglion (after Valentin). In one a second nucleus is visible. In several the nucleus contains one or two nucleoli.

† Fig. 139. Stellate or caudate nerve-corpuscles, with tubular processes issuing from them. Besides being filled with granular material continuous with the contents of the processes, the corpuscles contain black pigment-matter (after Hannover).

ment: the nucleus, which is vesicular, contains a nucleolus (fig. 138). Besides varying much in shape, partly in consequence of mutual pressure, they present such other varieties as make it probable either that there are two different kinds, or that, in the stages of their development, they pass through very different forms. Some of them are small, generally spherical or ovoid, and have a regular uninterrupted outline (fig. 138). These *simple* nerve-corpuscles are most numerous in the sympathetic ganglia. Others, which are called *caudate* or *stellate nerve-corpuscles* (fig. 139), are larger, and have one, two, or more long processes issuing from them, the cells being called respectively *unipolar, bipolar,* or *multipolar;* which processes often divide and subdivide, and appear tubular, and filled with the same kind of granular material that is contained within the corpuscle. Of these processes some appear to taper to a point and terminate at a greater or less distance from the corpuscle; some appear to anastomose with similar offsets from other corpuscles; while others are believed to become continuous with nerve-fibres, the prolongation from the cell by degrees assuming the characters of the nerve-fibre with which it is continuous.

Functions of Nerve-Fibres.

The office of the nerves as simple conveyors or conductors of nervous impressions is of a two-fold kind. First, they serve to convey to the nervous centres the impressions made upon their peripheral extremities, or parts of their course. Secondly, they serve to transmit impressions from the brain and other nervous centres to the parts to which the nerves are distributed.

For this two-fold office of the nerves, two distinct sets of nerve-fibres are provided, in both the cerebro-spinal and sympathetic systems. Those which convey impressions

from the periphery to the centre are classed together as *centripetal* or *afferent* nerves. Those fibres, on the other hand, which are employed to transmit central impulses to the periphery are classed as *centrifugal* or *efferent* nerves.

Centripetal or afferent nerve-fibres may (*a*) convey to the nerve-centres with which they are connected impressions which will give rise to *sensation* (*sensitive* nerves), or (*b*) they may convey an impression which travels out again from the nerve-centre by an efferent nerve-fibre, and produces some effect where the latter is distributed, (see Section on *Reflex* Action), or (*c*) they may convey an impression which will produce a restraining or *inhibitory* action in the nerve-centre, (*inhibitory* nerves, p. 131).

Centrifugal or efferent nerves may be (*a*) for the conveyance of impulses to the voluntary and involuntary muscles, (*motor* nerves,) or (*b*) they may influence nutrition (*trophic* nerves), (p. 388,) or (*c*) they may influence secretion (sometimes called *secretory* nerves) (p. 409).

With this difference in the functions of nerves, there is no apparent difference in the structure of the nerve-fibres by which it might be explained. Among the cerebro-spinal nerves, the fibres of the optic and auditory nerves are finer than those of the nerves of common sensation; but, with these exceptions, no centripetal fibres can be distinguished in their microscopic or general characters from those of centrifugal nerves.

Nerve-fibres possess no power of generating force in themselves, or of originating impulses to action: for the manifestation of their peculiar endowments they require to be stimulated. They possess a certain property of conducting impressions, a property which has been named excitability; but this is never manifested till some stimulus is applied. Thus, under ordinary circumstances, nerves of sensation are stimulated by external objects acting upon their extremities; and nerves of motion by the will, or

by some force generated in the nervous centres. But almost all things that can disturb the nerves from their passive state act as stimuli, and agents the most dissimilar produce the same kind, though not the same degree of effect, because that on which they act possesses but one kind of excitable force. Thus all stimuli—chemical, mechanical, and electric,—when applied to parts endowed with sensation, or to sensitive nerves (the connection of the latter with the brain and spinal cord being uninjured) produce sensations; and when applied to the nerves of muscles excite contractions. Muscular contraction is produced by such stimuli as well when the motor nerve is still in connection with the brain, as when its communication with the nervous centres is cut off by dividing it; nerves, therefore, have, by virtue of their excitability, the property of exciting contractions in muscles to which they are distributed; and the part of the divided motor nerve which is connected with the muscle will still retain this power, however much we may curtail it.

Mechanical irritation, when so violent as to injure the texture of the primitive nerve-fibres, deprives the centripetal nerves of their power of producing sensations when irritation is again applied at a point more distant from the brain than the injured spot; and in the same way, no irritation of a motor nerve will excite contraction of the muscle to which it is distributed, if the nerve has been compressed and bruised between the point of irritation and the muscle; the effect of such an injury being the same as that of division.

The action of nerves is also excited by *temperature*. Thus, when heat is applied to the nerve going to a muscle, or to the muscle itself, contractions are produced. These contractions are very violent when the flame of a candle is applied to the nerve, while less elevated degrees of heat,—for example, that of a piece of iron merely warmed,—do not irritate sufficiently to excite action of the muscles.

The application of cold has the same effect as that of heat. The effect of the local action of excessive or long-continued cold or heat on the nerves is the same as that of destructive mechanical irritation. The sensitive and motor power in the part is destroyed, but the other parts of the nerve retain their excitability; and, after the extremity of a divided nerve going to a muscle has been burnt, contractions of the muscle may be excited by irritating the nerve below the burnt part.

Chemical Stimuli excite the action of both afferent and efferent nerves as mechanical irritants do; provided their effect is not so strong as to destroy the structure of the nerve to which they are applied. A like manifestation of nervous power is produced by *electricity* and by *magnetism.*

Some of these laws regulating the excitability of nerves, and their power of manifesting their functions, require further notice, with several others which have not yet been alluded to. Certain of the laws and conditions of actions relate to nerves both centrifugal and centripetal, being dependent on properties common to all nerve-fibres; while of others, some are peculiar to nerves of motion, some to nerves of sensation.

It is a law of action in all nerve-fibres, and corresponds with the continuity and simplicity of their course, that an impression made on any fibre, is simply and uninterruptedly transmitted along it, without being imparted or diffused to any of the fibres lying near it. In other words, all nerve-fibres are mere *conductors* of impressions. Their adaptation to this purpose is, perhaps, due to the contents of each fibre being completely isolated from those of adjacent fibres by the membrane or sheath in which each is enclosed, and which acts, it may be supposed, just as silk, or other non-conductors of electricity do, which, when covering a wire, prevent the electric condition of the wire from being conducted into the surrounding medium.

Nervous force travels along nerve-fibres with considerable velocity. Helmholtz and Baxt have estimated the average rate of conduction of electrical impressions in human motor nerves at 111 feet per second: this result agreeing very closely with that previously obtained by Hirsch. Dr. Rutherford's observations agree with those of Von Wittich, that the rate of transmission in sensory nerves is about 140 feet per second.

Nerve-fibres convey only one kind of impression. Thus, a motor fibre conveys only motor impulses, that is, such as may produce movements in contractile parts: a sensitive fibre transmits none but such as may produce sensation, if they are propagated to the brain. Moreover, the fibres of a nerve of special sense, as the optic or auditory, convey only such impressions as may produce a peculiar sensation, *e.g.*, that of light or sound. While the rays of light and the sonorous vibrations of the air, are without influence on the nerves of common sensation, the other stimuli, which may produce pain when applied to them, produce, when applied to these nerves of special sense, only morbid sensations of light, or sound, or taste, according to the nerve impressed.

Of the laws of action peculiar to nerves of sensation and of motion respectively, many can be ascertained only by experiments on the roots of the nerves. For it is only at their origin that the nerves of sensation and of motion are distinct; their filaments, shortly after their departure from the nervous centres, are mingled together, so that nearly all nerves, except those of the special senses, consist of both sensitive and motor filaments, and are hence termed mixed nerves.

Nerves of *sensation* appear able to convey impressions only from the parts in which they are distributed, towards the nerve-centre from which they arise, or to which they tend. Thus, when a sensitive nerve is divided, and irrita-

tion is applied to the end of the proximal portion, *i.e.*, of the portion still connected with the nervous centre, sensation is perceived, or a reflex action ensues; but, when the end of the distal portion of the divided nerve is irritated, no effect appears.

When an impression is made upon any part of the course of a sensitive nerve, the mind may perceive it as if it were made not only upon the point to which the stimulus is applied, but also upon all the points in which the fibres of the irritated nerve are distributed: in other words, the effect is the same as if the irritation were applied to the parts supplied by the branches of the nerve. When the whole trunk of the nerve is irritated, the sensation is felt at all the parts which receive branches from it; but when only individual portions of the trunk are irritated, the sensation is perceived at those parts only which are supplied by the several portions. Thus, we if compress the ulnar nerve where it lies at the inner side of the elbow-joint, behind the internal condyle, we have the sensation of "pins and needles," or of a shock, in the parts to which its fibres are distributed, namely, in the palm and back of the hand, and in the fifth and ulnar half of the fourth finger. When stronger pressure is made, the sensations are felt in the fore-arm also; and if the mode and direction of the pressure be varied, the sensation is felt by turns in the fourth finger, in the fifth, and in the palm of the hand, or in the back of the hand, according as different fibres or fasciculi of fibres are more pressed upon than others.

It is in accordance with this law, that when parts are deprived of sensibility by compression or division of the nerve supplying them, irritation of the portion of the nerve connected with the brain still excites sensations which are felt as if derived from the parts to which the peripheral extremities of the nerve-fibres are distributed. Thus, there are cases of paralysis in which the limbs are totally insensible to external stimuli, yet are the seat of most

violent pain, resulting apparently from irritation of the sound part of the trunk of the nerve still in connection with the brain, or from irritation of those parts of the nervous centre from which the sensitive nerve or nerves which supply the paralysed limbs originate.

An illustration of the same law is also afforded by the cases in which division of a nerve for the cure of neuralgic pain is found useless, and in which the pain continues or returns, though portions of the nerve be removed. In such cases, the disease is probably seated nearer the nervous centre than the part at which the division of the nerve is made, or it may be in the nervous centre itself. When the cause of the neuralgia is seated in the trunk of the nerve—for example, of the facial or infra-orbital nerve—division of the branches can be of no service; for the stump remaining in connection with the brain, and containing all the fibres distributed in the branches of the nerve to the skin, continues to give rise, when irritated, to the same sensations as are felt when the peripheral parts themselves are affected. Division of a nerve prevents the possibility of external impressions on the cutaneous extremities of its fibre being felt; for these impressions can no longer be communicated to the brain: but the same sensations which were before produced by external impressions may arise from internal causes. In the same way may be explained the fact, that when part of a limb has been removed by amputation, the remaining portions of the nerves which ramified in it may give rise to sensations which the mind refers to the lost part. When the stump and the divided nerves are inflamed, or pressed, the patient complains of pain felt as if in the part which has been removed. When the stump is healed, the sensations which we are accustomed to have in a sound limb are still felt; and tingling and pains are referred to the parts that are lost, or to particular portions of them, as to single toes, to the sole of the foot, to the dorsum of the foot, etc.

But (as Volkmann shows) it must not be assumed, as it often has been, from these examples, that the mind has no power of discriminating the very point in the length of any nerve-fibre to which an irritation is applied. Even in the instances referred to, the mind perceives the pressure of a nerve at the point of pressure, as well as in the seeming sensations derived from the extremities of the fibres: and in stumps, pain is felt in the stump, as well as, seemingly, in the parts removed. It is not quite certain whether those sensations are perceived by the nerve-fibres which are on their way to be distributed elsewhere, or by the sentient extremities of nerves which are themselves distributed to the many trunks of the nerves, the nervi nervorum. The latter is the more probable supposition.

The habit of the mind to refer impressions received through the sensitive nerves to the parts from which impressions through those nerves are, or were, commonly received, is further exemplified when the relative position of the peripheral extremities of sensitive nerves is changed artificially, as in the transposition of portions of skin. When in the restoration of a nose, a flap of skin is turned down from the forehead and made to unite with the stump of the nose, the new nose thus formed has, as long as the isthmus of skin by which it maintains its original connections remains undivided, the same sensations as if it were still on the forehead; in other words, when the nose is touched, the patient feels the impression as if it were made on the forehead. When the communication of the nervous fibres of the new nose with those of the forehead is cut off by division of the isthmus of skin, the sensations are no longer referred to the forehead; the sensibility of the nose is at first absent, but is gradually developed.

When, in a part of the body which receives two sensitive nerves, one is paralysed, the other may or may not be inadequate to maintain the sensibility of the entire part; the extent to which the sensibility is preserved corresponding

probably with the number of the fibres unaffected by the paralysis. Thus when the ulnar nerve, which supplies the fifth and a part of the fourth finger, is divided, the sensibility of those parts is not preserved through the medium of the branches which the ulnar derives from the median nerve; but the fourth and fifth fingers are permanently deprived of sensibility. On the other hand, there are instances in which the trunk of the chief sensitive nerve supplied to a part having been divided, the sensibility of the part is still preserved by intercommunicating fibres from a neighbouring nerve-trunk. Thus, a case is related by Mr. Savory in which, after excision of a portion of the musculo-spiral nerve, the sensibility of some of the parts supplied by it, although impaired, was not altogether lost, probably on account of those fibres from the external cutaneous nerve which are mingled with the radial branch of the musculo-spiral. One of the uses of a nervous plexus (p. 470) is here well illustrated.

Several of the laws of action in *motor nerves* correspond with the foregoing. Thus, the motor influence is propagated only in the direction of the fibres going to the muscles; by irritation of a motor nerve, contractions are excited in all the muscles supplied by the branches given off by the nerve below the point irritated, and in those muscles alone: the muscles supplied by the branches which come off from the nerve at a higher point than that irritated, are never directly excited to contraction. No contraction, for instance, is produced in the frontal muscle by irritating the branches of the facial nerve that ramify upon the face; because that muscle derives its motor nerves from the trunk of the facial previous to these branches. So, again, because the isolation of motor nerve-fibres is as complete as that of sensitive ones, the irritation of a part of the fibres of the motor nerve does not affect the motor power of the whole trunk, but only that of the portion to which the stimulus is applied. And it is from

the same fact that, when a motor nerve enters a plexus and contributes with other nerves to the formation of a nervous trunk proceeding from the plexus, it does not impart motor power to the whole of that trunk, but only retains it isolated in the fibres which form its continuation in the branches of that trunk.

Functions of Nerve-Centres.

As already observed (p. 473), the term *nerve-centre* is applied to all those parts of the nervous system which contain ganglion-corpuscles, or vesicular nerve-substance, *i.e.*, the brain, spinal cord, and the several ganglia which belong to the cerebro-spinal and the sympathetic systems. Each of these nervous centres has a proper range of functions, the extent of which bears a direct proportion to the number of nerve-fibres that connect it with the various organs of the body, and with other nervous centres; but they all have certain general properties and modes of action common to them as nervous centres.

It is generally regarded as the property of nervous centres that they originate the impulses by which muscles may be excited to action, and by which the several functions of organic life may be maintained. Hence, they are often called *sources* or *originators* of nervous power or force. But the instances in which these expressions can be used are very few, and, strictly speaking, do not exist at all. The brain does not issue any force, except when itself impressed by some force from within, or stimulated by an impression from without; neither without such previous impressions do the other nerve-centres produce or issue motor impulses. The intestinal ganglia, for example, do not give out the nervous force necessary to the contractions of the intestines, except when they receive, through their centripetal nerves, the stimuli of substances in the intestinal

canal. So, also, the spinal cord; for a decapitated animal lies motionless so long as no irritation is applied to its centripetal nerves, though the moment they are touched movements ensue.

The more certain and general office of all the nervous centres is that of variously disposing and transferring the impressions that reach them through the several centripetal nerve-fibres. In nerve-fibres, as already said, impressions are only *conducted* in the simple isolated course of the fibre; in all the nervous centres an impression may be not only conducted, but also communicated: in the brain alone it may be *perceived*.

Conduction in or through *nerve-centres* may be thus simply illustrated. The food in a given portion of the intestines, acting as a stimulus, produces a certain impression on the nerves in the mucous membrane, which impression is conveyed through them to the adjacent ganglia of the sympathetic. In ordinary cases, the consequence of such an impression of the ganglia is the movement of the muscular coat of that and the adjacent part of the canal. But if irritant substances be mingled with the food, the sharper stimulus produces a stronger impression, and this is *conducted through* the nearest ganglia to others more and more distant; and, from all these, motor impulses issuing, excite a wide-extended and more forcible action of the intestines. Or even through all the sympathetic ganglia, the impression may be further conducted to the ganglia of the spinal nerves, and through them to the spinal cord, whence may issue motor impulses to the abdominal and other muscles, producing cramp. And yet further, the same morbid impression may be conducted through the spinal cord to the brain, where the mind may perceive it. In the opposite direction, mental influence may be conducted from the brain through a succession of nervous centres—the spinal cord and ganglia, and one or more ganglia of the sympathetic—to produce the influence

of the mind on the digestive and other organic functions. In short, in all cases in which the mind either has cognizance of, or exercises influence on, the processes carried on in any part supplied with sympathetic nerves, there must be a *conduction* of impressions through all the nervous centres between the brain and that part. It is probable that in this conduction through nervous centres the impression is not propagated through uninterrupted nerve-fibres, but is conveyed through successive nerve-vesicles and connecting nerve-filaments; and in some instances, and when the stimulus is exceedingly powerful, the conduction may be effected as quickly as through continuous nerve-fibres.

But instead of, or as well as, being conducted, impressions made on nervous centres may be *communicated* from the fibres that brought them, to others; and in this communication may be either *transferred*, *diffused*, or *reflected*.

The *transference of impressions* may be illustrated by the pain in the knee, which is a common sign of disease of the hip. In this case the impression made by the disease on the nerves of the hip-joint is conveyed to the spinal cord; there it is *transferred* to the central ends or connections of the nerve-fibres distributed about the knee. Through these the transferred impression is conducted to the brain, and the mind, referring the sensation to the part from which it usually through these fibres receives impressions, feels as if the disease and the source of pain were in the knee. At the same time that it is transferred, the primary impression may be also conducted; and in this case the pain is felt in both the hip and the knee. So, not unfrequently, if one touches a small pimple, that may be seated in the trunk, a pain will be felt in as small a spot on the arm, or some other part of the trunk. And so, in whatever part of the respiratory organs an irritation may be seated, the impression it produces is transferred to the nerves of the larynx; and then the mind perceives the peculiar sensation

of tickling in the glottis, which best, or almost alone, excites the act of coughing. Or, again, when the sun's light falls strongly on the eye, a tickling may be felt in the nose, exciting sneezing. In all these cases, the primary impression may be conducted as well as transferred; and in all it is transferred to a certain set of nerves which generally appear to be in some purposive relation with the nerves first impressed.

The *diffusion* or *radiation of impressions* is shown when an impression received at a nervous centre is diffused to many other fibres in the same centre, and produces sensations extending far beyond, or in an indefinite area around, the part from which the primary impression was derived. Hence, as in the former cases, result various kinds of what have been denominated sympathetic sensations. Sometimes such sensations are referred to almost every part of the body: as in the shock and tingling of the skin produced by some startling noise. Sometimes only the parts immediately surrounding the point first irritated participate in the effects of the irritation; thus, the aching of a tooth may be accompanied by pain in the adjoining teeth, and in all the surrounding parts of the face; the explanation of such a case being, that the irritation conveyed to the brain by the nerve-fibres of the deceased tooth is *radiated* to the central ends of adjoining fibres, and that the mind perceives this secondary impression as if it were derived from the peripheral ends of the fibres. Thus, also the pain of a calculus in the ureter is diffused far and wide.

All the preceding examples represent impressions communicated from one sensitive fibre to others of the same kind; or from fibres of special sense to those of common sensation. A similar communication of impressions from sensitive to motor fibres, constitutes *reflection* of impressions, displays the important functions common to all nervous centres as *reflectors*, and produces *reflex* movements. In the

extent and direction of such communications, also, phenomena corresponding to those of transference and diffusion to sensitive nerves, are observed in the phenomena of reflection. For, as in transference, the reflection may take place from a certain limited set of sensitive nerves to a corresponding and related set of motor nerves; as when in consequence of the impression of light on the retina, the iris contracts, but no other muscle moves. Or, as in diffusion or radiation, the reflection may bring widely-extended muscles into action: as when an irritation in the larynx brings all the muscles engaged in expiration into coincident movement.

It will be necessary, hereafter, to consider in detail so many of the instances of the reflecting power of the several nervous centres, that it may be sufficient here to mention only the most general rules of reflex action:—

1. For the manifestation of every reflex muscular action, three things are necessary; (1), one or more perfect centripetal nerve-fibres, to convey an impression; (2), a nervous centre to which this impression may be conveyed, and by which it may be reflected; (3), one or more centrifugal nerve-fibres, upon which this impression may be reflected, and by which it may be conducted to the contracting tissue. In the absence of any one of these three conditions, a proper reflex movement could not take place; and whenever impressions made by external stimuli on sensitive nerves give rise to motions, these are never the result of the direct reaction of the sensitive and motor fibres of the nerves on each other; in all such cases the impression is conveyed by the sensitive fibres to a nervous centre, and is therein communicated to the motor fibres.

2. All reflex actions are essentially involuntary, and may be accomplished independently of the will, though most of them admit of being modified, controlled, or prevented by a voluntary effort.

3. Reflex actions performed in health have, for the most

part, a distinct purpose, and are adapted to secure some end desirable for the well-being of the body; but, in disease, many of them are irregular and purposeless. As an illustration of the first point, may be mentioned movements of the digestive canal, the respiratory movements, and the contraction of the eyelids and the pupil to exclude many rays of light, when the retina is exposed to a bright glare. These and all other normal reflex acts afford also examples of the mode in which the nervous centres *combine* and arrange co-ordinately the actions of the nerve-fibres, so that many muscles may act together for the common end. Another instance of the same kind is furnished by the spasmodic contractions of the glottis on the contact of carbonic acid, or any foreign substance, with the internal substance of the epiglottis or larynx. Examples of the purposeless irregular nature of morbid reflex action are seen in the convulsive movements of epilepsy, and in the spasms of tetanus and hydrophobia.

4. Reflex muscular acts are often more sustained than those produced by the direct stimulus of muscular nerves. As Volkmann relates, the irritation of a muscular organ, or its motor nerve, produces contraction lasting only so long as the irritation continues; but irritation applied to a nervous centre through one of its centripetal nerves, may excite reflex and harmonious contractions, which last some time after the withdrawal of the stimulus.

CEREBRO-SPINAL NERVOUS SYSTEM.

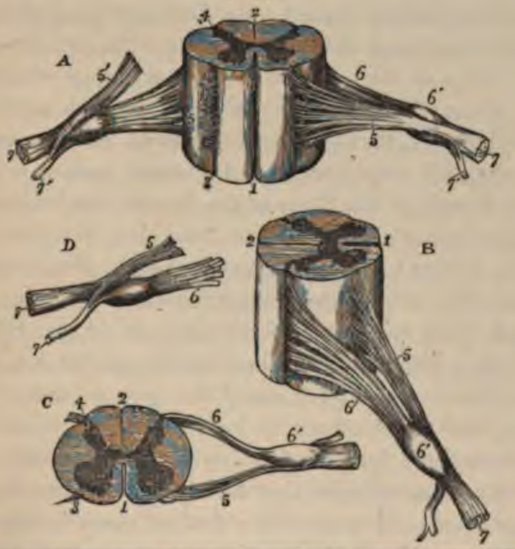
The physiology of the cerebro-spinal nervous system includes that of the spinal cord, medulla oblongata, and brain, of the several nerves given off from each, and of the

* Fig. 140. View of the cerebro-spinal axis of the nervous system (after Bourgery).—The right half of the cranium and trunk of the body has been removed by a vertical section; the membranes of the brain and spinal marrow have also been removed, and the roots and first part of the fifth and ninth cranial, and of all the spinal nerves of the right side, have been dissected out and laid separately on the wall of the

the lateral and posterior column arise the *posterior roots* of the same: a pair of roots on each side corresponding to each vertebra (fig. 141).

The fibrous part of the cord contains continuations of the innumerable fibres of the spinal nerves issuing from it, or entering it; but it is, probably, not formed of them exclu-

Fig. 141.*



* Fig. 141. Different views of a portion of the spinal cord from the cervical region, with the roots of the nerves slightly enlarged (from Quain). In A, the anterior suface of the specimen is shown; the anterior nerve-root of its right side being divided; in B, a view of the right side is given; in C the upper surface is shown; in D, the nerve-roots and ganglion are shown from below. 1, the anterior median fissure; 2, posterior median fissure; 3, anterior lateral depression, over which the anterior nerve-roots are seen to spread; 4, posterior lateral groove, into which the posterior roots are seen to sink; 5, anterior roots passing the ganglion; 5′, in A, the anterior root divided; 6, the posterior roots, the fibres of which pass into the ganglion 6′; 7, the united or compound nerve; 7′, the posterior primary branch, seen in A and D to be derived in part from the anterior and in part from the posterior root.

sively; nor is it a mere trunk, like a great nerve, through which they may pass to the brain. It is, indeed, among the most difficult things in structural anatomy to determine the course of individual nerve-fibres, or even of fasciculi of fibres, through even a short distance of the spinal cord; and it is only by the examination of transverse and longitudinal sections through the substance of the cord, such as those so successfully made by Mr. Lockhart Clarke, that we can obtain anything like a correct idea of the direction taken by the fibres of the roots of the spinal nerves within the cord. From the information afforded by such sections it it would appear, that of the root-fibres of the nerve which enter the cord, some assume a transverse, others a longitudinal direction: the fibres of the former pass horizontally or obliquely into the substance of the cord, in which many of them appear to become continuous with fibres entering the cord from other roots; others pass into the columns of the cord, while some perhaps terminate at or near the part which they enter: of the fibres of the second set, which usually first traverse a portion of the grey substance, some pass upwards, and others, at least of the posterior roots, turn downwards, but how far they proceed in either direction, or in what manner they terminate, are questions still undetermined. It is probable that of these latter, many constitute longitudinal commissures, connecting different segments of the cord with each other; while others, probably, pass directly to the brain.

The general rule respecting the size of different parts of the cord appears to be, that the size of each part bears a direct proportion to the size and number of nerve-roots given off from itself, and has but little relation to the size or number of those given off below it. Thus the cord is very large in the middle and lower part of its cervical portion, whence arise the large nerve-roots for the formation of the brachial plexuses and the supply of the upper extremities, and again enlarges at the lowest part of its

dorsal portion and the upper part of its lumbar, at the origins of the large nerves which, after forming the lumbar and sacral plexuses, are distributed to the lower extremities. The chief cause of the greater size at these parts of the spinal cord is increase in the quantity of grey matter; for there seems reason to believe that the white or fibrous part of the cord becomes gradually and progressively larger from below upwards, doubtless from the addition of a certain number of upward passing fibres from each pair of nerves.

It may be added, however, that there is no sufficient evidence for the supposition that an uninterrupted continuity of nerve-fibres is essential to the conduction of impressions on the spinal nerves to and from the brain: such impressions may be as well transmitted through the nerve-vesicles of the cord as by the nerve-fibres; and the experiments of Brown-Séquard, again to be alluded to, make it probable that the grey substance of the cord is the only channel through which sensitive impressions are conveyed to the brain.

The *Nerves of the Spinal Cord* consist of thirty-one pairs, issuing from the sides of the whole length of the cord, their number corresponding with the intervertebral foramina through which they pass. Each nerve arises by two roots, an anterior and posterior, the latter being the larger. The roots emerge through separate apertures of the sheath of dura mater surrounding the cord; and directly after their emergence, where the roots lie in the intervertebral foramen, a ganglion is found on the posterior root. The anterior root lies in contact with the anterior surface of the ganglion, but none of its fibres intermingle with those in the ganglion. But immediately beyond the ganglion the two roots coalesce, and by the mingling of their fibres form a compound or mixed spinal nerve, which, after issuing from the intervertebral canal, divides into an

anterior and posterior branch, each containing fibres from both the roots (fig. 141).

According to Kölliker the posterior root-fibres of the cord enter into no connection with the nerve-corpuscles in the ganglion, but pass directly through, in one or more bundles, which are collected into a trunk beyond the ganglion, and then join the motor root. From most, if not all, of the ganglionic corpuscles, one or two, rarely more, nerve-fibres arise and pass out of the ganglion, in a peripheral direction, in company with the posterior root-fibres of the cord. Each spinal ganglion, therefore, is to be regarded as a source of new nerve-fibres, which Kölliker names *ganglionic fibres.* The destination of these fibres is not yet determined: probably they pass especially into the vascular branches of the nerves which they accompany.

The anterior root of each spinal nerve arises by numerous separate and converging fasciculi from the anterior column of the cord; the posterior root by more numerous parallel fasciculi, from the posterior column, or, rather, from the posterior part of the lateral column; for if a fissure be directed inwards from the groove between the middle and posterior columns, the posterior roots will remain attached to the former. The anterior roots of each spinal nerve consist exclusively of motor fibres; the posterior as exclusively of sensitive fibres. For the knowledge of this important fact, and much of the consequent progress of the physiology of the nervous system, science is indebted to Sir Charles Bell. The fact is proved in various ways. Division of the anterior roots of one or more nerves is followed by complete loss of motion in the parts supplied by the fibres of such roots; but the sensation of the same parts remains perfect. Division of the posterior roots destroys the sensibility of the parts supplied by their fibres, while the power of motion continues unimpaired. Moreover, irritation of the ends of the distal portions of the divided anterior roots of a nerve excites

muscular movements; irritation of the ends of the proximal portions, which are still in connection with the cord, is followed by no effect. Irritation of the distal portions of the divided posterior roots, on the other hand, produces no muscular movements and no manifestation of pain; for, as already stated, sensitive nerves convey impressions only towards the nervous centres: but irritation of the proximal portions of these roots elicit signs of intense suffering. Occasionally, under this last irritation, muscular movements also ensue; but these are either voluntary, or the result of the irritation being reflected from the sensitive to the motor fibres. Occasionally, too, irritation of the distal ends of divided anterior roots elicits signs of pain, as well as producing muscular movements: the pain thus excited is probably the result of *cramp* (Brown-Séquard).

As an example of the experiments of which the preceding paragraph gives a summary account, this may be mentioned: If in a frog the three posterior roots of the nerves going to the hinder extremity be divided on the left side, and the three anterior roots of the corresponding nerves on the right side, the left extremity will be deprived of sensation, the right of motion. If the foot of the right leg, which is still endowed with sensation but not with the power of motion, be cut off, the frog will give evidence of feeling pain by movements of all parts of the body except the right leg itself, in which he feels the pain. If, on the contrary, the foot of the left leg, which has the power of motion, but is deprived of sensation, is cut off, the frog does not feel it, and no movement follows, except the twitching of the muscles irritated by cutting them or their tendons.

Functions of the Spinal Cord.

The spinal cord manifests all the properties already assigned to nerve centres (see p. 483).

1. It is capable of conducting impressions, or states of

nervous excitement. Through it, the impressions made upon the peripheral extremities or other parts of the spinal sensitive nerves are conducted to the brain, where alone they can be perceived by the mind. Through it, also, the stimulus of the will, applied to the brain, is capable of exciting the action of the muscles supplied from it with motor nerves. And for all these conductions of impressions to and fro between the brain and the spinal nerves, the perfect state of the cord is necessary; for when any part of it is destroyed, and its communication with the brain is interrupted, impressions on the sensitive nerves given off from it below the seat of injury, cease to be propagated to the brain, and the mind loses the power of voluntarily exciting the motor nerves proceeding from the portion of cord isolated from the brain.

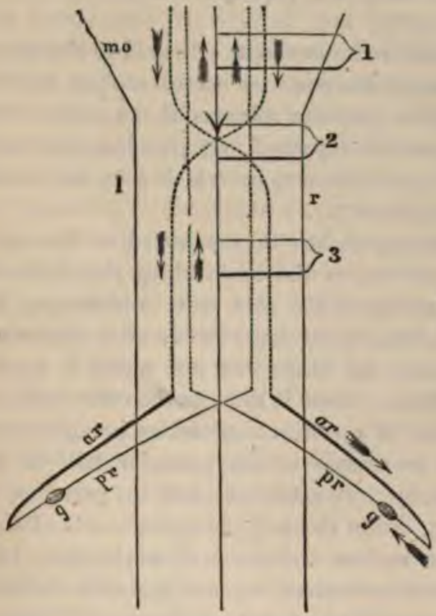
Illustrations of this are furnished by various examples of paralysis, but by none better than by the common paraphlegia, or loss of sensation and voluntary motion in the lower part of the body, in consequence of destructive disease or injury of a portion, including the whole thickness, of the spinal cord. Such lesions destroy the communication between the brain and all parts of the spinal cord below the seat of injury, and consequently cut off from their connection with the mind the various organs supplied with nerves issuing from those parts of the cord. But if this lower portion of the cord preserves its integrity, the various parts of the body supplied with nerves from it, though cut off from the brain, will nevertheless be subject to the influence of the cord, and, as presently to be shown, will indicate its other powers as a nervous centre.

From what has been already said, it will appear probable that the conduction of impressions along the cord is effected (at least, for the most part) through the grey substance, *i.e.*, through the nerve-corpuscles and filaments connecting them. But there is reason to believe that all parts of the cord are not alike able to conduct all impressions; and

that, rather, as there are separate nerve-fibres for motor and for sensitive impressions, so in the cord, separate and determinate parts serve to conduct always the same kind of impression.

The important and philosophical labours of Dr. Brown-

Fig. 142.*



* The above diagram (after Brown-Séquard) represents the decussation of the conductors for voluntary movements, and those for sensation: *a*, *r*, anterior roots and their contiuations in the spinal cord, and decussation at the lower part of the medulla oblongata, *m o*; *p r*, the posterior roots and their continuation and decussation in the spinal cord; *g g*, the ganglions of the roots. The arrows indicate the direction of the nervous action; *r*, the right side; *l*, the left side. 1, 2, 3, indicate places of alteration in a lateral half of the spino-cerebral axis, to show the influence on the two kinds of conductors, resulting from section of the cord at any one of these three places.

Séquard have cast much new light on all relating to the functions of the spinal cord. It is not possible to do justice to these investigations in any summary, however lengthy and complete: the whole series (delivered in lectures at the College of Surgeons,) must be read and studied. An attempt will be made here to point out only the principal conclusions deducible from them.

a. Sensitive impressions, conveyed to the spinal cord by root-fibres of the posterior nerves are not conducted to the brain by the posterior columns of the cord, as hitherto has been generally supposed, but pass through them into the central grey substance, by which they are transmitted to the brain (fig. 142).

b. The impressions thus conveyed to the grey substance do not pass up to the brain along that half of the cord corresponding to the side from which they have been received, but, almost immediately after entering the cord, cross over to the other side, and along it are transmitted to the brain. There is thus, in the cord itself, a complete decussation of sensitive impressions brought to it; so that division or disease of one posterior half of the cord is followed by lost sensation, not in parts on the corresponding, but in those of the opposite side of the body.

c. The various sensations of touch, pain, temperature, and muscular contraction, are probably conducted along separate and distinct sets of fibres. All, however, with the exception of the last named, undergo decussation in the spinal cord, and along it are transmitted to the brain by the grey matter.

d. The posterior columns of the cord appear to have a great share in reflex movements, and this is the principal cause of the peculiar kind of paralysis so often observed in disease of these columns.

e. Impulses of the will, leading to voluntary contractions of muscles, appear to be transmitted principally along the

anterior columns, and the contiguous grey matter of the cord.

f. Decussation of motor impulses occurs, not in the spinal cord, as is the case with sensitive impressions, but, as hitherto admitted, at the anterior part of the medulla oblongata. This decussation, however, does not take place, as generally supposed, all along the median line, at the base of the encephalon, but only at that portion of the anterior pyramids, which is continuous with the lateral columns of the cord. Hence, the mandates of the will, having made their decussation, first enter the cord by the lateral tracts and adjoining grey matter, and then pass to the anterior columns and to the grey matter associated with them. Accordingly, division of the anterior pyramids, at the point of decussation, is followed by paralysis of motion in all parts below; while division of the olivary bodies, which constitute the true continuations of the anterior columns of the cord, appears to produce very little paralysis. Disease or division of any part of the cerebro-spinal axis *above* the seat of decussation is followed, as well-known, by impaired or lost power of motion on the *opposite* side of the body; while a like injury inflicted *below* this part, induces similar paralysis on the *corresponding* side.

2. In the second place, the spinal cord as a nerve-centre, or rather as an aggregate of many nervous centres, has the power of *communicating impressions* in the several ways already mentioned (p. 485).

Examples of the *transference* and *radiation* of impressions in the cord have been given; and that the transference at least takes place in the cord, and not in the brain, is nearly proved by the case of pain felt in the knee and not in the hip, in diseases of the hip; of pain felt in the urethra or glans penis, and not in the bladder, in calculus; for, if both the primary and the secondary or transferred impressions were in the brain, both should be always felt. Of

radiations of impressions, there are, perhaps, no means of deciding whether they take place in the spinal cord or in the brain; but the analogy of the cases of transference makes it probable that the communication is, in this also, effected in the cord.

The power, as a nerve-centre, of communicating impressions from sensitive to motor, or, more strictly, from centripetal to centrifugal nerve-fibres, is what is usually discussed as the *reflex* function of the spinal cord. Its general mode of action, its general though incomplete independence of consciousness and of the will, and the conditions necessary for its perfection, have been already stated. These points, and the extent to which the power operates in the production of the natural *reflex movements* of the body, have now to be further illustrated. They will be described in terms adapted to the general rules of reflection of impressions in nervous centres, avoiding all such terms as might seem to imply that the power of the spinal cord in reflecting, is different in kind from that of all other nervous centres.

The occurrence of movements under the influence of the spinal cord, and independent of the will, is well exemplified in the acts of swallowing, in which a portion of food carried by voluntary efforts into the fauces, is conveyed by successive involuntary contractions of the constrictors of the pharynx and muscular walls of the œsophagus into the stomach. These contractions are excited by the stimulus of the food on the centripetal nerves of the pharynx and œsophagus being first conducted to the spinal cord and medulla oblongata, and thence reflected through the motor nerves of these parts. All these movements of the pharynx and œsophagus are involuntary; the will cannot arrest them or modify them; and though the mind has a certain consciousness of the food passing, which becomes less as the food passes further, yet that this is not necessary to the act of deglutition, is shown by its occurring

when the influence of the mind is completely removed; as when food is introduced into the fauces or pharynx during a state of complete coma, or in a brainless animal.

So also, for example, under the influence of the spinal cord, the involuntary and unfelt muscular contraction of the *sphincter ani* is maintained when the mind is completely inactive, as in deep sleep, but ceases when the lower part of the cord is destroyed, and cannot be maintained by the will.

The independence of the mind manifested by the reflecting power of the cord, is further shown in the perfect occurrence of the reflex movements when the spinal cord and the brain are disconnected, as in decapitated animals, and in cases of injuries or diseases so affecting the spinal cord as to divide or disorganize its whole thickness at any part whose perfection is not essential to life. Thus, when the head of a lizard is cut off, the trunk remains standing on the feet, and the body writhes when the skin is irritated. If the animal be cut in two, the lower portion can be excited to motion as well as the upper portion: the tail may be divided into several segments, and each segment, in which any portion of spinal cord is contained, contracts on the slightest touch; even the extremity of the tail moves as before, as soon as it is touched. All the portions of the animal in which these movements can be excited, contain some part of the spinal cord; and it is evidently the cause of the motions excited by touching the surface; for they cannot be excited in parts of the animal, however large, if no part of the cord is contained in them. Mechanical irritation of the skin excites not the slightest motion in the leg when it is separated from the body; yet the extremity of the tail moves as soon as it is touched. The same power of the spinal cord in reflecting impressions will cause an eel, or a frog, or any other cold-blooded animal, to move along after it is deprived of its head, and when, however much the movements may indicate purpose, it is not

probable that consciousness or will has any share in them. And so, in the human subject, or any warm-blooded animal, when the cord is completely divided across, or so diseased at some part that the influence of the mind cannot be conveyed to the parts below it, the irritation of any part of the surface supplied by nerves given off from the cord below the seat of injury, is commonly followed by spasmodic and irregular reflex movements, even though in the healthy state of the cord, such involuntary movements could not be excited when the attention of the mind was directed to the irritating cause.

In the fact last mentioned, is an illustration of an important difference between the warm-blooded and the lower animals, in regard to the reflecting power of the spinal cord (or its homologue in the Invertebrata), and the share which it and the brain have, respectively, in determining the several natural movements of the body. When, for example, a frog's head is cut off, the limbs remain in, or assume, a natural position; resume it when disturbed; and when the abdomen or back is irritated, the feet are moved with the manifest purpose of pushing away the irritation. It is as if the mind of the animal were still engaged in the acts.* But, in division of the human spinal cord, the lower extremities fall into any position that their weight and the resistance of surrounding objects combine to give them; if the body is irritated, they do not move towards the irritation; and if themselves are touched, the consequent movements are disorderly and purposeless. Now, if

* The evident adaptation and purpose in the movements of the cold-blooded animals, have led some to think that they must be conscious and capable of will without their brains. But purposive movements are no proof of consciousness or will in the creature manifesting them. The movements of the limbs of headless frogs are not more purposive than the movements of our own respiratory muscles are; in which we know that neither will nor consciousness is at all times concerned.

we are justified by analogy in assuming that the will of the frog cannot act more than the will of man, through the spinal cord separated from the brain, then it must be admitted that many more of the natural and purposive movements of the body can be performed under the sole influence of the cord in the frog than in man; and what is true in the instance of these two species, is generally true also of the whole class of cold-blooded, as distinguished from warm-blooded, animals. It may not, indeed, be assumed that the acts of standing, leaping, and other movements, which decapitated cold-blooded animals can perform, are also always, in the entire and healthy state, performed involuntarily, and under the sole influence of the cord; but it is probable that such acts may be, and commonly are, so performed, the higher nerve-centres of the animal having only the same kind of influence in modifying and directing them, that those of man have in modifying and directing the movements of the respiratory muscles.

The fact that such movements as are produced by irritating the skin of the lower extremities in the human subject, after division or disorganization of a part of the spinal cord, do not follow the same irritation when the mind is active and connected with the cord through the brain, is, probably, due to the mind ordinarily perceiving the irritation and instantly controlling the muscles of the irritated and other parts; for, even when the cord is perfect, such involuntary movements will often follow irritation, if it be applied when the mind is wholly occupied. When, for example, one is anxiously thinking, even slight stimuli will produce involuntary and reflex movements. So, also, during sleep, such reflex movements may be observed when the skin is touched or tickled; for example, when one touches with the finger the palm of the hand of a sleeping child, the finger is grasped—the impression on the skin of the palm producing a reflex movement of the muscles which

close the hand. But when the child is awake, no such effect is produced by a similar touch.

On the whole, it may, from these and like facts, be concluded that the proper reflex acts, performed under the influence of the reflecting power of the spinal cord, are essentially independent of the brain, and may be performed perfectly when the brain is separated from the cord:* that these include a much larger number of the natural and purposive movements of the lower animals than of the warm-blooded animals and man: and that over nearly all of them the mind may exercise, through the brain, some control; determining, directing, hindering, or modifying them, either by direct action or by its power over associated muscles.

In this fact, that the reflex movements from the cord may be perfectly performed without the intervention of consciousness or will, yet are amenable to the control of the will, we may see their admirable adaptation to the well-being of the body. Thus, for example, the respiratory movements may be performed while the mind is, in other things, fully occupied, or in sleep powerless; yet in an emergency, the mind can direct and strengthen them: and it can adapt them to the several acts of speech, effort, etc. Being, for ordinary purposes, independent of the will and consciousness, they are performed perfectly, without experience or education of the mind; yet they may be employed for other and extraordinary uses when the mind wills, and so far as it acquires power over them. Being commonly independent of the brain, their constant continuance does not produce weariness; for it is only in the brain that it or any other sensation can be perceived.

The subjection of the muscles to both the spinal cord

* Reflex movements, occurring quite independently of sensation, are generally called *excito-motor;* those which are guided or accompanied by sensation, but not to the extent of a distinct perception or intellectual process, are termed *sensori-motor.*

and the brain, makes it difficult to determine in man what movements or what share in any of them can be assigned to the reflecting power of the cord. The fact that after division or disorganization of a part of the cord, movements, and even forcible though purposeless ones, are produced in the lower limbs when the skin is irritated, proves that the spinal cord can reflect a stimulus to the action of the muscles that are, naturally, most under the control of the will: and it is, therefore, not improbable that, for even the involuntary action of those muscles, when the cord is perfect, it may supply the nervous stimulus, and the will the direction. As instances in which it supplies both stimulus and direction, that is, both excites and determines the combination of muscles, may be mentioned the acts of the abdominal muscles in vomiting and voiding the contents of the bladder and rectum: in both of which, though, after the period of infancy, the mind may have the power of postponing or modifying the act, there are all the evidences of reflex action; namely, the necessary precedence of a stimulus, the independence of the will, and, sometimes, of consciousness, the combination of many muscles, the perfection of the act without the help of education or experience, and its failure or imperfection in disease of the lower part of the cord. The emission of semen is equally a reflex act governed by the spinal cord: the irritation of the glans penis conducted to the spinal cord, and thence reflected, excites the successive and co-ordinate contractions of the muscular fibres of the vasa deferentia and vesiculæ seminales, and of the accelerator urinæ and other muscles of the urethra; and a forcible expulsion of semen takes place, over which the mind has little or no control, and which, in cases of paraplegia, may be unfelt. The erection of the penis, also, as already explained (p. 185), appears to be in part the result of a reflex contraction of the muscles by which the veins returning the blood from the penis are compressed. Irritation of the vagina in sexual intercourse

appears also to be propagated to the spinal cord, and thence reflected to the motor nerves supplying the Fallopian tubes. The involuntary action of the uterus in expelling its contents during parturition, is also of a purely reflex kind, dependent in part upon the spinal cord, though in part also upon the sympathetic system: its independence of the brain being proved by cases of delivery in paraplegic women, and now more abundantly shown in the use of chloroform.

Besides these acts regularly performed under the influence of the reflecting power of the spinal cord, others are manifested in accidents, such as the movement of the limbs and other parts to guard the body against the effects of sudden danger. When, for example, a limb is pricked or struck, it is instantly and involuntarily withdrawn from the instrument of injury; and the same preservative tendency of the reflex power of the cord is shown in the outstretched arms when falling forwards, and their reversed position when falling backwards; the action, although apparently voluntary, being really, in most cases, only an instance of reflex action.

To these instances of spinal reflex action, some add yet many more, including nearly all the acts which seem to be performed unconsciously, such as those of walking, running, writing, and the like: for these are really involuntary acts. It is true that at their first performances they are voluntary, that they require education for their perfection, and are at all times so constantly performed in obedience to a mandate of the will, that it is difficult to believe in their essentially involuntary nature. But the will really has only a *controlling* power over their performance; it can hasten or stay them, but it has little or nothing to do with the actual carrying out of the effect. And this is proved by the circumstance that these acts can be performed with complete mental abstraction: and, more than this, that the endeavour to carry them out entirely by the exercise of the

will is not only not beneficial, but positively interferes with their harmonious and perfect performance. Anyone may convince himself of this fact by trying to take each step as a voluntary act in walking down stairs, or to form each letter or word in writing by a distinct exercise of the will.

These actions, however, will be again referred to, when treating of their possible connection with the functions of the so-called *sensory ganglia* (p. 523).

The phenomena of spinal reflex actions in man are much more striking and unmixed in cases of disease. In some of these, the effect of a morbid irritation, or a morbid irritability of the cord, is very simple; as when the local irritation of sensitive fibres, being propagated to the spinal cord, excites merely local spasms,—spasms, namely, of those muscles, the motor fibres of which arise from the same part of the spinal cord as the sensitive fibres that are irritated. Of such a case we have instances in the involuntary spasmodic contraction of muscles in the immediate neighbourhood of inflamed joints; and numerous other examples of a like kind might be quoted.

In other instances, in which we must assume that the cord is morbidly more irritable, *i.e.*, apt to issue more nervous force than is proportionate to the stimulus applied to it, a slight impression on a sensitive nerve produces extensive reflex movements. This appears to be the condition in tetanus, in which a slight touch on the skin may throw the whole body into convulsion. A similar state is induced by the introduction of strychnia, and, in frogs, of opium, into the blood; and numerous experiments on frogs thus made tetanic, have shown that the tetanus is wholly unconnected with the brain, and depends on the state induced in the spinal cord.

It may seem to have been implied that the spinal cord, as a single nervous centre, reflects alike from all parts all the impressions conducted to it. But it is more probable that

it should be regarded as a collection of nervous centres united in a continuous column. This is made probable by the fact that segments of the cord may act as distinct nervous centres, and excite motions in the parts supplied with nerves given off from them; as well as by the analogy of certain cases in which the muscular movements of single organs are under the control of certain circumscribed portions of the cord. Thus Volkmann has shown that the rhythmical movements of the anterior pair of lymphatic hearts in the frog depend upon nervous influence derived from the portion of spinal cord corresponding to the third vertebra, and those of the posterior pair on influence supplied by the portion of cord opposite the eighth vertebra. The movements of the heart continue, though the whole of the cord, except the above portions, be destroyed; but on the instant of destroying either of these portions, though all the rest of the cord be untouched, the movements of the corresponding hearts cease. What appears to be thus proved in regard to two portions of the cord, may be inferred to prevail in other portions also; and the inference is reconcilable with most of the facts known concerning the physiology and comparative anatomy of the cord.

The influence of the spinal cord on the sphincter ani has been already mentioned (p. 501). It maintains this muscle in permanent contraction, so that, except in the act of defecation, the orifice of the anus is always closed. This influence of the cord resembles its common reflex action in being involuntary, although the will can act on the muscle to make it contract more or to permit its dilatation, and in that the constant action of the muscle is not felt, nor diminished in sleep, nor productive of fatigue. But the act is different from ordinary reflex acts in being nearly constant. In this respect it resembles that condition of muscles which has been called *tone,** or passive contraction; in a state in

* This kind of tone must be distinguished from that mere firmness

which they always appear to be when not active in health, and in which, though called inactive, they appear to be in slight contraction, and certainly are not relaxed, as they are long after death, or when the spinal cord is destroyed. This tone of all the muscles of the trunk and limbs seems to depend on the spinal cord, as the contraction of the sphincter ani does. If an animal be killed by injury or removal of the brain, the tone of the muscles may be felt, and the limbs feel firm as during sleep; but if the spinal cord be destroyed, the sphincter ani relaxes, and all the muscles feel loose, and flabby, and atonic, and remain so till the rigor mortis commences.

THE MEDULLA OBLONGATA.

Its Structure.

The medulla oblongata is a mass of grey and white nervous substance partly contained within the cavity of the cranium,—forming a portion of the cephalic prolongation of the spinal cord and connecting it with the brain. The grey substance which it contains is situated in the interior, and variously divided into masses and laminæ by the white or fibrous substance which is arranged partly in external columns, and partly in fasciculi traversing the central grey matter. The medulla oblongata is larger than any part of the spinal cord. Its columns are pyriform, enlarging as they proceed towards the brain, and are continuous with those of the spinal cord.

Each half of the medulla, therefore, may be divided into three columns or tracts of fibres, continuous with the three

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and tension which it is customary to ascribe, under the name of *tone*, to all tissues that feel robust and not flabby, as well as to muscles. The tone peculiar to muscles has in it a degree of vital contraction: that of other tissues is only due to their being well nourished, and therefore compact and tense.

tracts of which each half of the spinal cord is made up. The columns are more prominent than those of the spinal cord, and separated from each other by deeper grooves. The *anterior*, continuous with the anterior columns of the cord, are called the anterior *pyramids*; the *posterior*, continuous with the posterior columns of the cord, are called the *restiform*

Fig. 143.*

Fig. 144.†

* Fig. 143. View of the anterior surface of the pons Varolii, and medulla oblongata. *a*, *a*, anterior pyramids. *b*, their decussation; *c*, *c*, olivary bodies; *d*, *d*, restiform bodies; *e*, arciform fibres; *f*, fibres described by Solly as passing from the anterior column of the cord to the cerebellum; *g*, anterior column of the spinal cord; *h*, lateral column; *p*, pons varolii; *i*, its upper fibres; 5, 5, roots of the fifth pair of nerves.

† Fig. 144. View of the posterior surface of the pons varolii, corpora quadrigemina, and medulla oblongata. The peduncles of the cerebellum are cut short at the side. *a*, *a*, the upper pair of corpora quadrigemina; *b*, *b*, the lower; *f*, *f*, superior peduncles of the cerebellum; *c*, eminence connected with the nucleus of the hypoglossal nerve; *e*, that of the glosso-pharyngeal nerve; *i*, that of the vagus nerve; *d*, *d*, restiform bodies; *p*, *p*, posterior pyramids; *v*, *v*, groove in the middle of the fourth ventricle, ending below in the calamus scriptorius; 7, 7, roots of the auditory nerves.

bodies; and the *lateral*, continuous with the lateral columns of the cord, are named simply from their position. On the fibres of the lateral column of each side, near its upper part, is a small oval mass containing grey matter, and named the *olivary body;* and at the posterior part of the restiform column, immediately on each side of the posterior median groove, a small tract is marked off by a slight groove from the remainder of the restiform body, and called the *posterior pyramid*. The restiform columns, instead of remaining parallel with each other throughout the whole of the medulla oblongata, diverge near its upper part, and by thus diverging, lay open, so to speak, a space called the fourth ventricle, the floor of which is formed by the grey matter of the interior of the medulla, by this divergence exposed.

On separating the anterior pyramids, and looking into the groove between them, some decussating fibres can be plainly seen.

Distribution of the Fibres of the Medulla Oblongata.

The *anterior pyramid* of each side, although mainly composed of continuations of the fibres of the anterior columns of the spinal cord, receives fibres from the lateral columns, both of its own and the opposite side; the latter fibres forming almost entirely those decussating strands before mentioned, which are seen in the groove between the anterior pyramids.

Thus composed, the anterior pyramidal fibres proceeding onwards to the brain are distributed in the following manner:—1. The greater part pass on through the pons to the cerebrum.* A portion of the fibres, however, run-

* The expressions "continuous fibres," and the like, appear to be usually understood as meaning that certain primitive nerve-fibres pass without interruption from one part to another. But such continuity of primitive fibres through long distances in the nervous centres is

ning apart from the others, joins some fibres from the olivary body, and unites with them to form what is called the *olivary fasciculus* or *fillet*. 2. A small tract of fibres proceeds to the cerebellum.

The *lateral column* on each side of the medulla, in proceeding upwards, divides into three parts, outer, inner, and middle, which are thus disposed of:—1. The *outer* fibres go with the restiform tract to the cerebellum. 2. The *middle* decussate across the middle line with their fellows, and form a part of the anterior pyramid of the opposite side. 3. The *inner* pass on to the cerebrum along the floor of the fourth ventricle, on each side, under the name of the *fasciculus teres*.

The fibres of the *restiform* body receive some small contributions from both the lateral and anterior columns of the medulla, and proceed chiefly to the cerebellum, but that small part behind, called *posterior pyramid*, is continued on with the fasciculus teres of each side along the floor of the fourth ventricle to the cerebrum.

As in structure, so also in the general endowments of their several parts, there is, probably, the closest analogy between the medulla oblongata and the spinal cord. The difference between them in size and form appears due, chiefly, first, to the divergence, enlargement, and decussation of the several columns, as they pass to be connected with the cerebellum or the cerebrum; and, secondly, to the insertion of new quantities of grey matter in the olivary bodies and other parts, in adaptation to the higher office

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very far from proved. The apparent continuity of fasciculi (which is all that dissection can yet trace) is explicable on the supposition that many comparatively short fibres lie parallel, with the ends of each inlaid among many others. In such a case, there would be an apparent continuity of fibres; just as there is, for example, when one untwists and picks out a long cord of silk or wool, in which each fibre is short, and yet each fasciculus appears to be continued through the whole cord.

and wider range of influence which the medulla oblongata as a nervous centre exercises.

Functions of the Medulla Oblongata.

In its functions the medulla oblongata differs from the spinal cord chiefly in the importance and extent of the actions that it governs. Like the cord, it may be regarded first, as *conducting* impressions, in which office it has a wider extent of function than any other part of the nervous system, since it is obvious that all impressions passing to and fro between the brain and the spinal cord and all nerves arising below the pons, must be transmitted through it. The decussation of part of the fibres of the anterior pyramids of the medulla oblongata explains the phenomena of cross-paralysis, as it is termed, *i.e.*, of the loss of motion in cerebral apoplexy, being always on the side opposite to that on which the effusion of blood has taken place. Looking only to the anatomy of the medulla oblongata, it was not possible to explain why the loss of sensation also is on the side opposite the injury or disease of the brain: for there is no evidence of a decussation of posterior fibres like that which ensues among the anterior fibres of the medulla oblongata. But the discoveries of Brown-Séquard have shown that the crossing of sensitive impressions occurs in the spinal cord (see p.498).

The functions of the medulla oblongata as a *nerve-centre* seem to be more immediately important to the maintenance of life than those of any other part of the nervous system, since from it alone, or in chief measure, appears to be reflected the nervous force necessary for the performance of respiration and deglutition. It has been proved by repeated experiments on the lower animals that the entire brain may be gradually cut away in successive portions, and yet life may continue for a considerable time, and the respiratory

movements be uninterrupted. Life may also continue when the spinal cord is cut away in successive portions from below upwards as high as the point of origin of the phrenic nerve, or in animals without a diaphragm, such as birds or reptiles, even as high as the medulla oblongata. In Amphibia, these two experiments have been combined: the brain being all removed from above, and the cord from below; and so long as the medulla oblongata was intact, respiration and life were maintained. But if, in any animal, the medulla oblongata is wounded, particularly if it is wounded in its central part, opposite the origin of the pneumogastric nerves, the respiratory movements cease, and the animal dies as if asphyxiated. And this effect ensues even when all parts of the nervous system, except the medulla oblongata, are left intact.

Injury and disease in men prove the same as these experiments on animals. Numerous instances are recorded in which injury to the human medulla oblongata has produced instantaneous death; and, indeed, it is through injury of it, or of the part of the cord connecting it with the origin of the phrenic nerve, that death is commonly produced in fractures and diseases with sudden displacement of the upper cervical vertebræ.

The centre whence the nervous force for the production of combined respiratory movements appears to issue is in the interior of that part of the medulla oblongata from which the pneumogastric nerves arise; for with care the medulla oblongata may be divided to within a few lines of this part, and its exterior may be removed without the stoppage of respiration; but it immediately ceases when this part is invaded. This is not because the integrity of the pneumogastric nerves is essential to the respiratory movements; for both these nerves may be divided without more immediate effect than a retardation of these movements. The conclusion, therefore, may safely be, that this part of the medulla oblongata is the nervous centre

whereby the impulses producing the respiratory movements are *reflected*.

The power by which the medulla oblongata governs and combines the action of various muscles for the respiratory movements, is an instance of the power of *reflexion*, which it possesses in common with all nervous centres. Its general mode of action, as well as the degree to which the mind may take part in respiration, and the number of nerves and muscles which, under the governance of the medulla oblongata, may be combined in the forcible respiratory movements, have been already briefly described (see p. 225, *et seq.*). That which seems most peculiar in this centre of respiratory action is its wide range of connection, the number of nerves by which the centripetal impression to excite motion may be conducted, and the number and distance of those through which the motor impulse may be directed. The principal centripetal nerves engaged in respiration are the pneumogastric, whose branches supplying the lungs appear to convey the most acute impression of the "necessity of breathing." When they are both divided, the respiration becomes slower (J. Reid), as if the necessity were less acutely felt: but it does not cease, and therefore other nerves besides them must have the power of conducting the like impression. The experiments of Volkmann make it probable that all centripetal nerves possess it in some degree, and that the existence of imperfectly aerated blood in contact with any of them acts as a stimulus, which, being conveyed to the medulla oblongata, is reflected to the nerves of the respiratory muscles: so that respiratory movements do not wholly cease so long as any centripetal nerves, and any nerve supplying muscles of respiration, are both in continuous connection with the respiratory centre of the medulla oblongata. The circulation of imperfectly aerated blood in the medulla oblongata itself may also act as a stimulus, and react through this nerve-centre on the nerves which supply the inspiratory muscles.

The wide extent of connection which belongs to the medulla oblongata as the centre of the respiratory movements, is further shown by the fact that impressions by mechanical and other ordinary stimuli, made on many parts of the external or internal surface of the body, may induce respiratory movements. Thus involuntary respirations are induced by the sudden contact of cold with any part of the skin, as in dashing cold water into the face. Irritation of the mucous membrane of the nose produces sneezing. Irritation in the pharynx, œsophagus, stomach, or intestines, excites the concurrence of the respiratory movements to produce vomiting. Violent irritation in the rectum, bladder, or uterus, gives rise to a concurrent action of the respiratory muscles, so as to effect the expulsion of the fæces, urine, or fœtus.

The medulla oblongata appears to be the centre whence are derived the motor impulses enabling the muscles of the palate, pharynx, and œsophagus, to produce the successive co-ordinate and adapted movements necessary to the act of *deglutition* (see p. 263). This is proved by the persistence of swallowing in some of the lower animals after destruction of the cerebral hemispheres and cerebellum; its existence in anencephalous monsters; the power of swallowing possessed by marsupial embryoes before the brain is developed; and by the complete arrest of the power of swallowing when the medulla oblongata is injured in experiments. But the reflecting power herein exercised by the medulla oblongata is of a much simpler and more restricted kind than that exercised in respiration; it is, indeed, not more than a simple instance of reflex action by a segment of the spinal axis, receiving impressions for this purpose from only a few centripetal nerves, and reflecting them to the motor nerves of the same organ. The incident or centripetal nerves in this case are the branches of the glossopharyngeal, and, in a subordinate degree, those of the fifth nerve, some of the branches of the superior laryn-

geal nerve, which are distributed to the pharynx; and the nerves through which the motor impressions to the fauces and pharynx are reflected, are the pharyngeal branches of the vagus, and, in subordinate degrees, or as supplying muscles accessory to the movements of the pharynx, the branches of the hypoglossal, facial, cervical, recurrent, and fifth nerves. For the œsophageal movements, so far as they are connected with the medulla oblongata, the filaments of the pneumogastric nerve alone, which contain both afferent and efferent fibres, appear to be sufficient (John Reid).

Though respiration and life continue while the medulla oblongata is perfect and in connection with respiratory nerves, yet, when all the brain above it is removed, there is no more appearance of sensation, or will, or of any mental act in the animal, the subject of the experiment, than there is when only a spinal cord is left. The movements are all involuntary and unfelt; and the medulla oblongata has, therefore, no claim to be considered as an organ of the mind, or as the seat of sensation or voluntary power. These are connected with parts next to be described.

It would appear that much of the reflecting power of the medulla oblongata may be destroyed; and yet its power in the respiratory movements may remain. Thus, in patients completely affected with chloroform, the winking of the eye-lids ceases, and irritation of the pharynx will not produce the usual movements of swallowing, or the closure of the glottis (so that blood may run quietly into the stomach, or even into the lungs); yet, with all this, they may breathe steadily, and show that the power of the medulla oblongata to combine in action all the nerves of the respiratory muscles is perfect.

In addition to its influence over the functions of respiration and deglutition, the medulla oblongata appears to be largely concerned also in the faculty of speech.

In the medulla oblongata appears to be seated also the chief *vaso-motor* nerve-centre (p. 576). From this arise fibres which, passing down the spinal cord, issue with the anterior roots of the spinal nerves, and enter the ganglia and branches of the sympathetic, by which they are conducted to the blood-vessels.

The influence which is exercised by the medulla oblongata, or, at least, by its irritation, on the formation of sugar in the liver, has been referred to (p. 336).

STRUCTURE AND PHYSIOLOGY OF THE PONS VAROLII, CRURA CEREBRI, CORPORA QUADRIGEMINA, CORPORA GENICULATA, OPTIC THALMI, AND CORPORA STRIATA.

Pons Varolii.—The meso-cephalon, or pons (VI, fig. 145), is composed principally of transverse fibres connecting the two hemispheres of the cerebellum, and forming its principal commissure. But it includes, interlacing with these, numerous longitudinal fibres which connect the medulla oblongata with the cerebrum, and transverse fibres which connect it with the cerebellum. Among the fasciculi of nerve-fibres by which these several parts are connected, the pons also contains abundant grey or vesicular substance, which appears irregularly placed among the fibres, and fills up all the interstices.

The anatomical distribution of the fibres, both transverse and longitudinal, of which the pons is composed, is sufficient evidence of its functions as a conductor of impressions from one part of the cerebro-spinal axis to another.

Concerning its functions as a nerve-centre, little or nothing is certainly known.

Crura Cerebri.—The *crura cerebri* (III, fig. 145), are principally formed of nerve-fibres, of which the inferior or more superficial are continuous with those of the anterior pyra-

midal tracts of the medulla oblongata, and the superior or deeper fibres with the lateral and posterior pyramidal tracts, and with the olivary fasiculus. Besides these fibres from the medulla oblongata, are others from the cerebellum; and

Fig. 145.*

some of the latter as well as a part of the fibres derived from the lateral tract of the medulla oblongata, decussate across the middle line.

* Fig. 145. Base of the brain (from Quain). ½.—1, superior longitudinal fissure; 2, 2', 2", anterior cerebral lobe; 3, fissure of Sylvius, between anterior and 4, 4,' 4", middle cerebral lobe; 5, 5', posterior lobe; 6, medulla oblongata; the figure is in the right anterior pyramid; 7, 8, 9, 10, the cerebellum; +, the inferior vermiform process. The figures from I. to IX. are placed against the corresponding cerebral nerves; III. is placed on the right crus cerebri; VI. and VII. on the pons Varolii; X. the first cervical or suboccipital nerve.

On their upper part, the crura cerebri bear three pairs of small ganglia, or masses of mingled grey and white nerve-substance, namely, the *corpora geniculata externa* and *interna*, and the *corpora quadrigemina*, or *nates* and *testes*. And in their onward course to the cerebrum, the fibres of each crus cerebi pass through two large ganglia, the *optic thalamus* and *corpus striatum*, and in their substance come into connection with variously-shaped masses and layers of grey substance. Whether all the fibres of the crura cerebri end in the grey matter of these two ganglia, while others start afresh from them to enter the cerebral hemispheres; or whether some of the fibres of the crura pass through them, while only a portion can be strictly said to have their termination there, must remain at present undecided; the difficulties in the way of solving such an anatomical doubt being at present insuperable.

Each crus cerebri contains among its fibres a mass of vesicular substance, the *locus niger*, the nerve-corpuscles of which abound in pigment-granules, and afford some of the best instances of the caudate structure.

With regard to their functions, the crura cerebri may be regarded as, principally, conducting organs. As nerve-centres they are probably connected with the functions of the third cerebral nerve, which arises from the *locus niger*, and through which are directed the chief of the numerous and complicated movements of the eyeball and iris.

From the result of vivisection it appears that when one of the crura cerebri is cut across, the animal moves round and round, rotating around a vertical axis from the injured towards the sound side. Such movements, however, attend the sections of other parts than the crura cerebri: and as indications of the functions of these parts, the results of such experiments have been hitherto almost valueless.

Corpora Quadrigemina.—The corpora quadrigemina (from

which, in function, the *corpora geniculata* are not distinguished), are the homologues of the optic lobes in birds, Amphibia and fishes, and may be regarded as the principal nervous centres for the sense of sight. The experiments of Flourens, Longet, and Hertwig, show that removal of the corpora quadrigemina wholly destroys the power of seeing; and diseases in which they are disorganized are usually accompanied with blindness. Atrophy of them is also often a consequence of atrophy of the eyes.

Destruction of one of the corpora quadrigemina (or of one optic lobe in birds), produces blindness of the opposite eye.

This loss of sight is the only apparent injury of sensibility sustained by the removal of the corpora quadrigemina. The removal of one of them affects the movements of the body, so that animals rotate, as after division of the crus cerebri, only more slowly: but this is probably due to giddiness and partial loss of sight. The more evident and direct influence is that produced on the iris. It contracts when the corpora quadrigemina are irritated: it is always dilated when they are removed: so that they may be regarded, in some measure at least, as the nervous centres governing its movements, and adapting them to the impressions derived from the retina through the optic nerves and tracts.

Concerning the functions, taken as a whole, discharged by the olfactory and optic lobes, the grey substance of the pons the corpora striata and optic thalami (*b*, *d*, fig. 146), with some other centres of grey matter not so distinct, such as the grey matter on the floor of the fourth ventricle with which the auditory nerve is connected, the most philosophical theory is undoubtedly that which has been so ably enunciated by Dr. Carpenter. He supposes these ganglia to constitute the real sensorium; that is to say, it is by means of them that the mind becomes conscious of impressions

made on the organs or tissues with which (by means of

Fig. 146.*

* Fig. 146. Dissection of brain, from above, exposing the lateral, fourth, and fifth ventricles, with the surrounding parts (from Hirschfeld and Leveillé). ½.—*a*, anterior part, or *genu* of corpus callosum; *b*, corpus striatum; *b'*, the corpus striatum of left side, dissected so as to expose its grey substance; *c*, points by a line to the tænia semicularis; *d*. optic thalamus; *e*, anterior pillars of fornix divided; below they are seen descending in front of the third ventricle, and between them is seen part of the anterior commissure; in front of the letter *e* is seen the slit-like fifth ventricle, between the two laminæ of the septum lucidum; *f*, soft or middle commissure; *g* is placed in the posterior part of the third ventricle; immediately behind the latter are the posterior commissure (just visible) and the pineal gland, the two crura of which extend forwards along the inner and upper margins of the optic Thalami; *h* and *i*, the corpora quadrigemina; *k*, superior crus of cerebellum; close to *k* is the valve of Vieussens, which has been divided so as to expose the fourth ventricle; *l*, hippocampus

nerve-fibres) they are in communication. Thus impressions made on the optic nerve, or its expansion in the retina, are conducted by the fibres of the optic nerve to the corpora quadrigemina, and through the medium of these ganglia the mind becomes conscious of the impression made. And impressions on the filaments of the olfactory or auditory nerve are in the same way perceived through the medium of the olfactory or auditory ganglia, to which they are first conveyed. The optic thalami and corpora striata probably have some function of a like kind —perhaps in relation to ordinary sensation, but nothing is certainly known regarding them.

Besides their functions, however, as media of communication between the mind and external objects, these *sensory ganglia*, as they are termed, are probably the nerve-centres by means of which those reflex acts are performed which require either a higher combination of muscular acts than can be directed by means of the medulla oblongata or spinal cord alone, or on the other hand, such reflex actions as require for their right performance the guidance of sensation. Under this head are included various acts, as walking, reading, writing, and the like, which we are accustomed to consider voluntary, but which really are as incapable of being performed by distinct and definite acts of the will as are those more simple movements of which we are not conscious, and which, performed under the guidance of the spinal cord or medulla oblongata alone, we call simple reflex actions. It is true that in the performance of such acts as those just-mentioned, a certain exercise of the will is required at the commencement, but that the carrying out of its mandates is essentially reflex

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major and corpus fimbriatum, or tænia hippocampi; *m*, hippocampus minor; *n*, eminentia collateralis; *o*, fourth ventricle; *p*, posterior surface of medulla oblongata; *r*, section of cerebellum; *s*, upper part of left hemisphere of cerebellum exposed by the removal of part of the posterior cerebral lobe.

and involuntary, anyone may convince himself by trying to perform each individual movement concerned, strictly as a voluntary act.

That such movements are reflex and essentially independent—as regards their mere production—of the will, there is no doubt: that the nerve-centres through which such reflex actions are performed are the so-called sensory ganglia, is, of course, only a theory which may or not be confirmed by future investigations.

Besides their possible functions in the manner just-mentioned, it is supposed that these sensory ganglia may be the means of transmitting the impulses of the will to the muscles, which act in obedience to it, and thus be the centres of reflex action as well for impressions conveyed *downwards* to them from the cerebral hemispheres, as for impressions carried *upwards* to them by the different nerves which preserve their connection with the organs of the various senses.

STRUCTURE AND PHYSIOLOGY OF THE CEREBELLUM.

The cerebellum (7, 8, 9, 10, fig. 147) is composed of an elongated central portion called the vermiform processes, and two hemispheres. Each hemisphere is connected with its fellow, not only by means of the vermiform processes, but also by a bundle of fibres called the *middle crus* or *peduncle* (the latter forming the greater part of the pons Varolii), while a *superior crus* with the valve of Vieussens, connects it with the cerebrum (fig. 147, 5), and an *inferior crus* (formed by the prolonged restiform body) connects it with the medulla oblongata (3, fig. 147).

The cerebellum is composed of white and grey matter like that of the cerebrum, but arranged after a different fashion as shown in fig. 147.

Besides the grey substances on the surface, however, there is near the centre of the white substance of each

hemisphere, a small capsule of grey matter called the *corpus dentatum* (fig. 148, *cd*), resembling very closely the

Fig. 147.

corpus dentatum of the olivary body of the medulla oblongata (fig. 148, *o*).

The physiology of the cerebellum may be considered in its relation to sensation, voluntary motion, and the instincts or higher faculties of the mind. It is itself insensible to irritation, and may be all cut away without eliciting signs

* Fig. 147. View of cerebellum in section and of fourth ventricle, with the neighbouring parts (from Sappey after Hirschfeld and Leveillé). 1, median groove of fourth ventricle, ending below in the *calamus scriptorius*, with the longitudinal eminences formed by the *fasciculi teretes* one on each side; 2, the same groove, at the place where the white streaks of the auditory nerve emerge from it to cros the floor of the ventricle; 3, inferior crus or peduncle of the cerebellum, formed by the restiform body; 4, posterior pyramid; above this is the calamus scriptorius; 5, superior crus of cerebellum, or processus a cerebello ad cerebrum (or ad testes); 6, 6, fillet to the side of the crura cerebri; 7, 7, lateral grooves of the crura cerebri; 8, corpora quadrigemina.

of pain (Longet). Yet, if any of its crura be touched, pain is indicated; and, if the restiform tracts of the medulla oblongata be irritated, the most acute suffering appears to be produced. Its removal or disorganization by disease is also generally unaccompanied with loss or disorder of sensibility; animals from which it is removed can smell, see, hear, and feel pain, to all appearance, as perfectly as

Fig. 148*.

before (Flourens; Magendie). So that, although the restiform tracts of the medulla oblongata, which themselves appear so sensitive, enter the cerebellum, it cannot be regarded as a principal organ of sensibility.

In reference to motion, the experiments of Longet and most others agree that no irritation of the cerebellum produces movement of any kind. Remarkable results,

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* Fig. 148. Outline sketch of a section of the cerebellum showing the corpus dentatum (from Quain). ¾.—The section has been carried through the left lateral part of the pons, so as to divide the superior peduncle and pass nearly through the middle of the left cerebellar hemisphere. The olivary body has also been divided longitudinally so as to expose in section its corpus dentatum. *c r*, crus cerebri; *f*, fillet; *q*, corpora quadrigemina; *s p*, superior peduncle of the cerebellum divided; *m p*, middle peduncle or lateral part of the pons Varolii, with fibres passing from it into the white stem; *a v*, continuation of the white stem radiating towards the arbor vitæ of the folia; *c d*, corpus dentatum; *o*, olivary body with its corpus dentatum; *p*, anterior pyramid.

however, are produced by removing parts of its substance. Flourens (whose experiments have been abundantly confirmed by those of Bouillaud, Longet, and others) extirpated the cerebellum in birds by successive layers. Feebleness and want of harmony of the movements were the consequence of removing the superficial layers. When he reached the middle layers, the animals became restless without being convulsed; their movements were violent and irregular, but their sight and hearing were perfect. By the time that the last portion of the organ was cut away, the animals had entirely lost the powers of springing, flying, walking, standing, and preserving their equilibrium. When an animal in this state was laid upon its back, it could not recover its former posture; but it fluttered its wings, and did not lie in a state of stupor; it saw the blow that threatened it, and endeavoured to avoid it. Volition, sensation, and memory, therefore, were not lost, but merely the faculty of combining the actions of the muscles; and the endeavours of the animal to maintain its balance were like those of a drunken man.

The experiments afforded the same results when repeated on all classes of animals; and, from them and the others before referred to, Flourens inferred that the cerebellum belongs neither to the sensitive nor the intellectual apparatus; and that it is not the source of voluntary movements, although it belongs to the motor-apparatus; but is the organ for the co-ordination of the voluntary movements, or for the excitement of the *combined* action of muscles.

Such evidence as can be obtained from cases of disease of this organ confirms the view taken by Flourens; and, on the whole, it gains support from comparative anatomy; animals whose natural movements require most frequent and exact combinations of muscular actions being those whose cerebella are most developed in proportion to the spinal cord.

M. Foville holds that the cerebellum is the organ of

muscular sense, i.e., the organ by which the mind acquires that knowledge of the actual state and position of the muscles which is essential to the exercise of the will upon them; and it must be admitted that all the facts just referred to are as well explained on this hypothesis as on that of the cerebellum being the organ for combining movements. A harmonious combination of muscular actions must depend as much on the capability of appreciating the condition of the muscles with regard to their tension, and to the force with which they are contracting, as on the power which any special nerve-centre may possess of exciting them to contraction. And it is because the power of such harmonious movement would be equally lost, whether the injury to the cerebellum involved injury to the seat of muscular sense, or to the centre for combining muscular actions, that experiments on the subject afford no proof in one direction more than the other.

Gall was led to believe, that the cerebellum is the organ of physical love, or, as Spurzheim called it, of amativeness; and this view is generally received by phrenologists. The facts favouring it are, first, several cases in which atrophy of the testes and loss of sexual passion have been the consequence of blows over the cerebellum, or wounds of its substance; secondly, cases in which disease of the cerebellum has been attended with almost constant erection of the penis, and frequent seminal emissions; and thirdly, that it has seemed possible to estimate the degree of sexual passion in different persons by an external examination of the region of the cerebellum.

The cases of disease of the cerebellum do not prove much; for the same affections of the genital organs are more generally observed in diseases, and in experimental irritations of the medulla oblongata and upper part of the spinal cord (Longet).

The facts drawn from craniological examination will receive the credit given to the system of which they are a

principal evidence. But, in opposition to them, it must be stated that there has been a case of complete disorganization or absence of the cerebellum without loss of sexual passion (Combiette, Longet, and Cruveilhier); that the cocks from whom M. Flourens removed the cerebellum showed sexual desire, though they were incapable of gratifying it; and that among animals there is no proportion observable between the size of the cerebellum and the development of the sexual passion. On the contrary, many instances may be mentioned in which a larger sexual appetite co-exists with a smaller cerebellum; as *e.g.*, that rays and eels, which are among the fish that copulate, have not laminæ on their almost rudimental cerebella; and that cod-fish, which do not copulate, but deposit their generative fluids in the water, have comparatively well-developed cerebella. Among the Amphibia, the sexual passion is apparently very strong in frogs and toads; yet the cerebellum is only a narrow bar of nervous substance. Among birds there is no enlargement of the cerebellum in the males that are polygamous; the domestic cock's cerebellum is not larger than the hen's, though his sexual passion must be estimated at many times greater than hers. Among Mammalia the same rule holds; and in this class the experiments of M. Lassaigne have plainly shown that the abolition of the sexual passion by removal of the testes in early life is not followed by any diminution of the cerebellum; for in mares and stallions the average absolute weight of the cerebellum is 61 grains, and in geldings 70 grains; and its proportionate weight, compared with that of the cerebrum, is, on average, as 1 : 6·59 in mares; as 1 : 5·97 in geldings, and only as 1 : 7·07 in stallions.

On the whole, therefore, it appears advisable to wait for more evidence before concluding that there is any peculiar and direct connection between the cerebellum and the sexual instinct or sexual passion. From all that has

been observed, no other office is manifest in it than that of regulating and combining muscular movements, or of enabling them to be regulated and combined by so informing the mind of the state and position of the muscles that the will may be definitely and aptly directed to them.

The influence of each half of the cerebellum is directed to muscles on the opposite side of the body; and it would appear that for the right ordering of movements, the actions of its two halves must be always mutually balanced and adjusted. For if one of its crura, or if the pons on either side of the middle line, be divided, so as to cut off from the medulla oblongata and spinal cord the influence of one of the hemispheres of the cerebellum, strangely disordered movements ensue. The animals fall down on the side opposite to that on which the crus cerebelli has been divided, and then roll over continuously and repeatedly; the rotation being always round the long axis of their bodies, and from the side on which the injury has been inflicted.* The rotations sometimes take place with much rapidity; as often, according to M. Magendie, as sixty times in a minute, and may last for several days. Similar movements have been observed in men; as by M. Serres in a man in whom there was apoplectic effusion in the right crus cerebelli; and by M. Belhomme in a woman, in whom an exostosis pressed on the left crus.† They

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* Magendie and Müller, and others following him, say the rotation is *towards* the injured side; but Longet and others more correctly give the statement as in the text. The difference has probably arisen from using the words *right* and *left*, without saying whose right and left are meant, whether those of the observer or those of the observed. When, for example, an animal's right crus cerebelli is divided, he rolls from his own right to his own left, but from the left to the right of one who is standing in front of him.

† See such cases collected and recorded by Dr. Paget in the Ed. Med. and Surg. Journal for 1847.

may, perhaps, be explained by assuming that the division or injury of the crus cerebelli produces paralysis or imperfect and disorderly movements of the opposite side of the body; the animal falls, and then, struggling with the disordered side on the ground, and striving to rise with the other, pushes itself over; and so, again and again, with the same act, rotates itself. Such movements cease when the other crus cerebelli is divided; but probably only because the paralysis of the body is thus made almost complete.

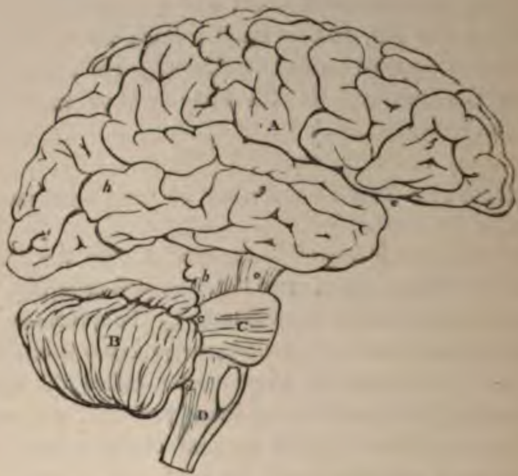
STRUCTURE AND PHYSIOLOGY OF THE CEREBRUM.

The cerebrum is placed in connection with the pons and medulla oblongata by its two *crura* or *peduncles* (fig. 149): it is connected with the cerebellum, by the processes called superior crura of the cerebellum, or *processus a cerebello ad testes*, and by a layer of grey matter, called the valve of Vieussens, which lies between these processes, and extends from the inferior vermiform process of the cerebellum to the corpora quadrigemina of the cerebrum. These parts, which thus connect the cerebrum with the other principal divisions of the cerebro-spinal nervous centre, form parts of the walls of a cavity (the fourth ventricle) and a canal (the *iter a tertio ad quartum ventriculum*), which are the continuation of the canal that in the fœtus extended through the whole length of the spinal cord and brain. They may, therefore, be regarded as the continuation of the cerebro-spinal axis or column; on which, as a development from the simple type, the cerebellum is placed; and, on the further continuation of which, structures both larger and more numerous are raised, to form the cerebrum (fig. 142).

The cerebral convolutions appear to be formed of nearly parallel plates of fibres, the ends of which are turned towards the surface of the brain, and are overlaid and

mingled with successive layers of grey nerve-substance. The external grey matter is so arranged in layers, that a vertical section of a convolution, according to Mr. Lockhart

Fig. 149.*



Clarke, generally presents the appearance of seven layers of pale and dark nervous substance. The structure of the grey matter is that which belongs to vesicular nervous substance (p. 473).

It is nearly certain that the cerebral hemispheres are the organ by which,—1*st*, we perceive those clear and more impressive sensations which we can retain, and

* Fig. 149. Plan in outline of the encephalon, as seen from the right side. ⅓. (From Quain).—The parts are represented as separated from one another somewhat more than natural, so as to show their connections. A, cerebrum; *f*, *g*, *h*, its anterior, middle, and posterior lobes; *e*, fissure of Sylvius; B, cerebellum; C, pons Varolii; D, medulla oblongata; *a*, peduncles of the cerebrum; *b*, *c*, *d*, superior, middle, and inferior peduncles of the cerebellum.

according to which we can judge; *2ndly*, by which are performed those acts of will, each of which requires a deliberate, however quick, determination; *3rdly*, they are the means of retaining impressions of sensible things, and reproducing them in subjective sensations and ideas; *4thly*, they are the medium of the higher emotions and feelings, and of the faculties of judgment, understanding, memory, reflection, induction, and imagination, and others of a like class.

The evidences that the cerebral hemispheres have the functions indicated above, are chiefly these:—1. That any severe injury of them, such as a general concussion, or sudden pressure by apoplexy, may instantly deprive a man of all power of manifesting externally any mental faculty. 2. That in the same general proportion as the higher sensuous mental faculties are developed in the vertebrate animals, and in man at different ages, the more is the size of the cerebral hemispheres developed in comparison with the rest of the cerebro-spinal system. 3. That no other part of the nervous system bears a corresponding proportion to the development of the mental faculties. 4. That congenital and other morbid defects of the cerebral hemisphere are, in general, accompanied with corresponding deficiency in the range or power of the intellectual faculties and the higher instincts.

Respecting the mode in which the brain discharges its functions, there is no evidence whatever. But it appears that, for all but its highest intellectual acts, one of the cerebral hemispheres is sufficient. For numerous cases are recorded in which no mental defect was observed, although one cerebral hemisphere was so disorganised or atrophied that it could not be supposed capable of discharging its functions. The remaining hemisphere was, in these cases, adequate to the functions generally discharged by both; but the mind does not seem in any of these cases to have been tested in very high intellectual

exercises; so that it is not certain that one hemisphere will suffice for these. In general, the mind combines, as one sensation, the impressions which it derives from one object through both hemispheres, and the ideas to which the two such impressions give rise are single.

In relation to common sensation and the effort of the will, the impressions to and from the hemispheres of the brain are carried across the middle line; so that in destruction or compression of either hemisphere, whatever effects are produced in loss of sensation or voluntary motion, are observed on the side of the body opposite to that on which the brain is injured.

In speaking of the cerebral hemispheres as the so-called organs of the mind, they have been regarded as if they were single organs, of which all parts are equally appropriate for the exercise of each of the mental faculties. But it is possible that each faculty has a special portion of the brain appropriated to it as its proper organ. For this theory the principal evidences are as follows:—1. That it is in accordance with the physiology of the other compound organs or systems in the body, in which each part has its special function; as, for example, of the digestive system, in which the stomach, liver, and other organs perform each their separate share in the general process of the digestion of the food. 2. That in different individuals the several mental functions are manifested in very different degrees. Even in early childhood, before education can be imagined to have exercised any influence on the mind, children exhibit various dispositions—each presents some predominant propensity, or evinces a singular aptness in some study or pursuit; and it is a matter of daily observation that every one has his peculiar talent or propensity. But it is difficult to imagine how this could be the case, if the manifestation of each faculty depended on the whole of the brain: different conditions of the whole mass might affect the mind generally, depressing or exalting all its functions

in an equal degree, but could not permit one faculty to be strongly and another weakly manifested. 3. The plurality of organs in the brain is supported by the phenomena of some forms of mental derangement. It is not usual for all the mental faculties in an insane person to be equally disordered; it often happens that the strength of some is increased, while that of others is diminished; and in many cases one function only of the mind is deranged, while all the rest are performed in a natural manner. 4. The same opinion is supported by the fact that the several mental faculties are developed to their greatest strength at different periods of life, some being exercised with great energy in childhood, others only in adult age; and that, as their energy decreases in old age, there is not a gradual and equal diminution of power in all of them at once, but, on the contrary, a diminution in one or more, while others retain their full strength, or even increase in power. 5. The plurality of cerebral organs appears to be indicated by the phenomena of dreams, in which only a part of the mental faculties are at rest or asleep, while the others are awake, and, it is presumed, are exercised through the medium of the parts of the brain appropriated to them.

These facts have been so illustrated and adapted by phrenologists, that the theory of the plurality of organs in the cerebrum, thus made probable, has been commonly regarded as peculiar to phrenology, and as so essentially connected with it, that if the system of Gall and Spurzheim be untrue, this theory cannot be maintained. But it is plain that all the system of phrenology built upon the theory may be false, and the theory itself true; for phrenologists assume, not only this theory, but also that they have determined all the primitive faculties, of which the mind consists, *i.e.*, all the faculties to which special organs must be assigned, and the places of all those organs in the cerebral hemispheres and the cerebellum.

That this is a system of error there need be no doubt, but it is possibly founded on a true theory: the cerebrum may have many organs, and the mind as many faculties; but what are the faculties that require separate organs, and where those organs are situate, are subjects of which only the most general and rudimentary knowledge has been yet attained.

From the apparently greater frequency of interference with the faculty of speech in disease of the *left* than of the *right* half of the cerebrum, it has been thought that the nerve-centre for *language*, including in this term all intellectual expression of ideas, is situate in the *left* cerebral hemisphere. It cannot be said, however, that the existing evidence for this theory is at present sufficient to have established it.

Of the physiology of the other parts of the brain, little or nothing can be said.

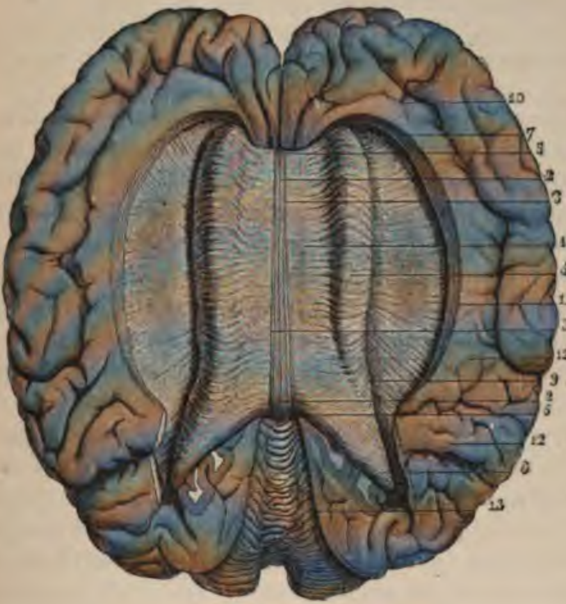
Of the offices of the *corpus callosum*, or great transverse and oblique commissure of the brain, nothing positive is known. But instances in which it was absent, or very deficient, either without any evident mental defect, or with only such as might be ascribed to coincident affections of other parts, make it probable that the office which is commonly assigned to it, of enabling the two sides of the brain to act in concord, is exercised only in the highest acts of which the mind is capable. And this view is confirmed by the very late period of its development, and by its absence in all but the placental Mammalia.*

To the fornix and other commissures no special function can be assigned; but it is a reasonable hypothesis that they connect the action of the parts between which they are severally placed.

* See cases of congenital deficiency of the corpus callosum, by Mr Paget and Mr. Henry in the twenty-ninth and thirty-first volumes of the Medico-Chirurgical Transactions.

As little is known of the function of the pineal and

Fig. 150.*



* Fig. 150. View of the corpus callosum from above (from Sappey after Foville). ½.—The upper surface of the corpus callosum has been fully exposed by separating the cerebral hemispheres and throwing them to the side; the gyrus fornicatus has been detached, and the transverse fibres of the corpus callosum traced for some distance into the cerebral medullary substance. 1, the upper surface of the corpus callosum; 2, median furrow or raphe; 3, longitudinal striæ bounding the furrow; 4, swelling formed by the transverse bands as they pass into the cerebrum; 5, anterior extremity or knee of the corpus callosum; 6, posterior extremity; 7, anterior, and 8, posterior part of the mass of fibres proceeding from the corpus callosum; 9, margin of the swelling; 10, anterior part of the convolution of the corpus callosum; 11, hem or band of union of this convolution; 12, internal convolutions of the parietal lobe; 13, upper surface of the cerebellum.

pituitary glands. The latter has been supposed, from its microscopic structure, to be rather a ductless gland (p. 410) than a nervous organ.

PHYSIOLOGY OF THE CEREBRAL AND SPINAL NERVES.

The cerebral nerves are commonly enumerated as nine pairs; but the number is in reality twelve, the seventh nerve consisting, as it does, of two nerves, and the eighth of three. These and the spinal nerves, of which there are thirty-one pairs, symmetrically arranged on each side of what, reduced to its simplest form, may be regarded as a column or axis of nervous matter, extending from the olfactory bulbs on the ethmoid bone to the *filum terminale* of the spinal cord in the lumbar and sacral portions of the vertebral canal. The spinal nerves all present certain characters in common, such as their double roots; the isolation of the fibres of sensation in the posterior roots, and those of motion in the anterior roots; the formation of the ganglia on the posterior root; and the subsequent mingling of the fibres in trunks and branches of mixed functions. Similar characters probably belong essentially to the cerebral nerves; but even when one includes the nerves of special sense, it is not possible to discern a conformity of arrangement in any besides the fifth, or trifacial, which, from its many analogies to the spinal nerves, Sir Charles Bell designed as a spinal nerve of the head.

According to their several functions, the cerebral or cranial nerves may be thus arranged:—

Nerves of special sense .	Olfactory, optic, auditory, part of the glosso-pharyngeal, and the lingual branch of the fifth.
,, of common sensation	The greater portion of the fifth, and part of the glosso-pharyngeal.

Nerves of motion . .	Third, fourth, lesser division of the fifth, sixth, facial, and hypoglossal.
Mixed nerves . . .	Pneumogastric, and accessory.

The physiology of the several nerves of the special senses will be considered with the organs of those senses.

Physiology of the Third, Fourth, and Sixth Cerebral or Cranial Nerves.

The physiology of these nerves may be in some degree combined, because of their intimate connection with each other in the actions of the muscles of the eyeball, which they supply. They are probably all formed exclusively of motor fibres: some pain is indicated when the trunk of the third nerve is irritated near its origin; but this may be because of some filaments of the fifth nerve running backwards to the brain in the trunk of the third, or because adjacent sensitive parts are involved in the irritation.

The third nerve, or *motor oculi*, supplies the levator palpebræ superioris muscle, and, of the muscles of the eyeball, all but the superior oblique or trochlearis, to which the fourth nerve is appropriated, and the rectus externus which receives the sixth nerve. Through the medium of the ophthalmic or lenticular ganglion, of which it forms what is called the short root, it also supplies the motor filaments to the iris.

When the third nerve is irritated within the skull, all those muscles to which it is distributed are convulsed. When it is paralyzed or divided, the following effects ensue: first, the upper eyelid can be no longer raised by the levator palpebræ, but drops and remains gently closed over the eye, under the unbalanced influence of the orbicularis palpebrarum, which is supplied by the facial nerve: secondly, the eye is turned outwards by the unbalanced action of the rectus externus, to which the sixth nerve is appropriated: and hence, from the irregularity of the axes

of the eyes, double-sight is often experienced when a single object is within view of both the eyes: thirdly, the eye cannot be moved either upwards, downwards, or inwards; fourthly, the pupil is dilated.

The relation of the third nerve to the iris is of peculiar interest. In ordinary circumstances the contraction of the iris is a reflex action, which may be explained as produced by the stimulus of light on the retina being conveyed by the optic nerve to the brain (probably to the corpora quadrigemina), and thence reflected through the third nerve to the iris. Hence the iris ceases to act when either the optic or the third nerve is divided or destroyed, or when the corpora quadrigemina are destroyed or much compressed. But when the optic nerve is divided, the contraction of the iris may be excited by irritating that portion of the nerve which is connected with the brain; and when the third nerve is divided, the irritation of its distal portion will still excite contraction of the iris in which its fibres are distributed.

The contraction of the iris thus shows all the character of a reflex act, and in ordinary cases requires the concurrent action of the optic nerve, corpora quadrigemina, and third nerve; and, probably also, considering the peculiarities of its perfect mode of action, the ophthalmic ganglion. But, besides, both irides will contract their pupils under the reflected stimulus of light falling only on one retina or under irritation of one optic nerve. Thus, in amaurosis of one eye, its pupil may contract when the other eye is exposed to a stronger light: and generally the contraction of each of the pupils appears to be in direct proportion to the total quantity of light which stimulates either one or both retinæ, according as one or both eyes are open.

The iris acts also in association with certain other muscles supplied by the third nerve: thus, when the eye is directed inwards, or upwards and inwards, by the action of the third nerve distributed in the rectus internus and

rectus superior, the iris contracts, as if under direct voluntary influence. The will cannot, however, act on the iris alone through the third nerve; but this aptness to contract in association with the other muscles supplied by the third, may be sufficient to make it act even in total blindness and insensibility of the retina, whenever these muscles are contracted. The contraction of the pupils, when the eyes are moved inwards, as in looking at a near object, has probably the purpose of excluding those outermost rays of light which would be too far divergent to be refracted to a clear image on the retina; and the dilatation in looking straight forwards, as in looking at a distant object, permits the admission of the largest number of rays, of which none are too divergent to be so refracted.

The fourth nerve, or *Nervus trochlearis* or *patheticus*, is exclusively motor, and supplies only the trochlearis or obliquus superior muscle of the eyeball.

The sixth nerve, *Nervus abducens* or *ocularis externus*, is also, like the fourth, exclusively motor, and supplies only the rectus externus muscle.* The rectus externus is, therefore, convulsed, and the eye is turned outwards, when the sixth nerve is irritated; and the muscle paralyzed when the nerve is disorganized, compressed, or divided. In all such cases of paralysis, the eye squints inwards, and cannot be moved outwards.

In its course through the cavernous sinus, the sixth nerve forms larger communications with the sympathetic nerve than any other nerve within the cavity of the skull does. But the import of these communications with the sympathetic, and the subsequent distribution of its fila-

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* In several animals it sends filaments to the iris (Radclyffe Hall); and it has probably done so in man, in some instances in which the iris has not been paralyzed, while all the other parts supplied by the third nerve were (Grant).

ments after joining the sixth nerve, are quite unknown; and there is no reason to believe that the sixth nerve is, in function, more closely connected with the sympathetic than any other cerebral nerve is.

The question has often suggested itself why the six muscles of the eyeball should be supplied by three motor nerves when all of them are within reach of the branches of one nerve; and the true explanation would have more interest than attaches to the movements of the eye alone; since it is probable that we have, in this instance, within a small space, an example of some general rule according to which associate or antagonist muscles are supplied with motor nerves.

Now, in the several movements of the eyes, we sometimes have to act with symmetrically-placed muscles, as when both eyes are turned upwards or downwards, inwards or outwards.* All the symmetrically-placed muscles are supplied with symmetrical nerves, *i.e.*, with corresponding branches of the same nerves on the two sides; and the action of these symmetrical muscles is easy and natural, as we have a natural tendency to symmetrical movement in most parts. But because of this tendency to symmetrical movements of muscles supplied by symmetrical nerves, it would appear as if, when the two eyes are to be moved otherwise than symmetrically, the muscles to effect such a movement must be supplied with different nerves. To, when the two eyes are to be turned towards one side, say the right, by the action of the rectus externus of the right eye and the rectus internus of the left, it appears as if the tendency to action through the similar branches of corresponding nerves (which would move both eyes inwards or outwards) were corrected by one of these muscles

* It is sometimes said, that the external recti cannot be put in action simultaneously: yet they are so when the eyes, having been both directed inwards, are restored to the position which they have in looking straight forwards.

being supplied by the sixth, and the other by the third nerve. So with the oblique muscles: the simplest and easiest actions would be through branches of the corresponding nerves, acting similarly as symmetrical muscles; but the necessary movements of the two eyes require the contraction of the superior oblique of one side, to be associated with the contraction of the inferior oblique and the relaxation of the superior oblique, of the opposite side. For this, the fourth nerve of one side is made to act with a branch of the third nerve of the other; as if thus the tendency to simultaneous action through the similar nerves of the two sides were prevented. At any rate, the rule of distribution of nerves here seems to be, that when in frequent and necessary movements any muscle has to act with the antagonist of its fellow on the opposite side, it and its fellow's antagonist are supplied from different nerves.

Physiology of the Fifth or Trigeminal Nerve.

The fifth or trigeminal nerve resembles, as already stated, the spinal nerves, in that its branches are derived through two roots; namely, the larger or *sensitive*, in connection with which is the Gasserian ganglion, and the smaller or *motor* root which has no ganglion, and which passes under the ganglion of the sensitive root to join the third branch or division which issues from it. The first and second divisions of the nerve, which arise wholly from the larger root, are purely sensitive. The third division being joined, as before said, by the motor root of the nerve, is of course both motor and sensitive.

Through the branches of the greater or ganglionic portion of the fifth nerve, all the anterior and antero-lateral parts of the face and head, with the exception of the skin of the parotid region (which derives branches from the cervical spinal nerves), acquire common sensibility; and among these parts may be included the organs of special

sense, from which common sensations are conveyed through the fifth nerve, and their peculiar sensation through their several nerves of special sense. The muscles, also, of the face and lower jaw acquire muscular sensibility through the filaments of the ganglionic portion of the fifth nerve distributed to them with their proper motor nerves.

Through branches of the lesser or non-ganglionic portion of the fifth, the muscles of mastication, namely, the temporal, masseter, two pterygoid, anterior part of the digastric, and mylo-hyoid, derive their motor nerves. The motor function of these branches is proved by the violent contraction of all the muscles of mastication in experimental irritation of the third, or inferior maxillary, division of the nerve; by paralysis of the same muscles, when it is divided or disorganized, or from any reason deprived of power; and by the retention of the power of these muscles, when all those supplied by the facial nerve lose their power through paralysis of that nerve. The last instance proves best, that though the buccinator muscle gives passage to, and receives some filaments from, a buccal branch of the inferior division of the fifth nerve, yet it derives its motor power from the facial, for it is paralysed together with the other muscles that are supplied by the facial, but retains its power when the other muscles of mastication are paralyzed. Whether, however, the branch of the fifth nerve which is supplied to the buccinator muscle is entirely sensitive, or in part motor also, must remain for the present doubtful. From the fact that this muscle, besides its other functions, acts in concert or harmony with the muscles of mastication, in keeping the food between the teeth, it might be supposed from analogy, that it would have a motor branch from the same nerve that supplies them. There can be no doubt, however, that the so-called buccal branch of the fifth, is, in the main, sensitive; although it is not quite certain that it may not give a few motor filaments to the buccinator muscle.

The sensitive function of the branches of the greater division of the fifth nerve is proved by all the usual evidences, such as their distribution in parts that are sensitive and not capable of muscular contraction, the exceeding sensibility of some of these parts, their loss of sensation when the nerve is paralyzed or divided, the pain without convulsions produced by morbid or experimental irritation of the trunk or branches of the nerve, and the analogy of this portion of the fifth to the posterior root of the spinal nerve.

But although formed of sensitive filaments exclusively, the branches of the greater or ganglionic portion of the fifth nerve exercise a manifold influence on the movements of the muscles of the head and face, and other parts in which they are distributed. They do so, in the first place, by providing the muscles themselves with that sensibility without which the mind, being unconscious of their position and state, cannot voluntarily exercise them. It is, probably, for conferring this sensibility on the muscles, that the branches of the fifth nerve communicate so frequently with those of the facial and hypoglossal, and the nerves of the muscles of the eye; and it is because of the loss of this sensibility that when the fifth nerve is divided, animals are always slow and awkward in the movement of the muscles of the face and head, or hold them still, or guide their movements by the sight of the objects towards which they wish to move.

Again, the fifth nerve has an indirect influence on the muscular movements, by conveying sensations of the state and position of the skin and other parts: which the mind perceiving, is enabled to determine appropriate acts. Thus, when the fifth nerve or its infra-orbital branch is divided, the movements of the lips in feeding may cease, or be imperfect; a fact which led Sir Charles Bell into one of the very few errors of his physiology of the nerves. He supposed that the motion of the upper lip, in grasping food,

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depended directly on the infra-orbital nerve; for he found that, after he had divided that nerve on both sides in an ass, it no longer seized the food with its lips, but merely pressed them against the ground, and used the tongue for the prehension of the food. Mr. Mayo corrected this error. He found, indeed, that after the infra-orbital nerve had been divided, the animal did not seize its food with the lip, and could not use it well during mastication, but that it could open the lips. He, therefore, justly attributed the phenomena in Sir C. Bell's experiments to the loss of sensation in the lips; the animal not being able to feel the food, and, therefore, although it had the power to seize it, not knowing how or where to use that power.

Lastly, the fifth nerve has an intimate connection with muscular movements through the many reflex acts of muscles of which it is the necessary excitant. Hence, when it is divided, and can no longer convey impressions to the nervous centres to be thence reflected, the irritation of the conjunctiva produces no closure of the eye, the mechanical irritation of the nose excites no sneezing, that of the tongue no flowing of saliva; and although tears and saliva may flow naturally, their afflux is not increased by the mechanical or chemical or other stimuli, to the indirect or reflected influence of which it is liable in the perfect state of this nerve.

The fifth nerve, through its ciliary branches and the branch which forms the long root of the ciliary or ophthalmic ganglion, exercises also some influence on the movements of the iris. When the trunk of the ophthalmic portion is divided, the pupil becomes, according to Valentin, contracted in men and rabbits, and dilated in cats and dogs; but in all cases, becomes immovable, even under all the varieties of the stimulus of light. How the fifth nerve thus affects the iris is unexplained; the same effects are produced by destruction of the superior cervical ganglion of the sympathetic, so that, possibly, they are due to the

injury of those filaments of the sympathetic which, after joining the trunk of the fifth, at and beyond the Gasserian ganglion, proceed with the branches of its ophthalmic division to the iris; or, as Dr. R. Hall ingeniously suggests, the influence of the fifth nerve on the movements of the iris may be ascribed to the affection of vision in consequence of the disturbed circulation or nutrition in the retina, when the normal influence of the fifth nerve and ciliary ganglion is disturbed. In such disturbance, increased circulation making the retina more irritable might induce extreme contraction of the iris; or, under moderate stimulus of light, producing partial blindness, might induce dilatation: but it does not appear why, if this be the true explanation, the iris should in either case be immovable and unaffected by the various degrees of light.

Furthermore, the morbid effects which division of the fifth nerve produces in the organs of special sense, make it probable that, in the normal state, the fifth nerve exercises some indirect influence on all these organs or their functions. Thus, after such division, within a period varying from twenty-four hours to a week, the cornea begins to be opaque; then it grows completely white; a low destructive inflammatory process ensues in the conjunctiva, sclerotica, and interior parts of the eye; and within one or a few weeks, the whole eye may be quite disorganized, and the cornea may slough or be penetrated by a large ulcer. The sense of smell (and not merely that of mechanical irritation of the nose), may be at the same time lost, or gravely impaired; so may the hearing, and commonly, whenever the fifth nerve is paralyzed, the tongue loses the sense of taste in its anterior and lateral parts, *i.e.*, in the portion in which the lingual or gustatory branch of the inferior maxillary division of the fifth is distributed.*

* That complete paralysis of the fifth nerve may, however, be unaccompanied, at least, for a considerable period, by injury to the organs

The loss of the sense of taste is no doubt chiefly due to the lingual branch of the fifth nerve being a nerve of special sense; partly, also, perhaps, it is due to the fact that this branch supplies, in the anterior and lateral parts of the tongue, a necessary condition for the proper nutrition of that part. But, deferring this question until the glosso-pharyngeal nerve is to be considered, it may be observed that in some brief time after complete paralysis or division of the fifth nerve, the power of all the organs of the special senses may be lost; they may lose not merely their sensibility to common impressions, for which they all depend directly on the fifth nerve, but also their sensibility to the several peculiar impressions for the reception and conduction of which they are purposely constructed and supplied with special nerves besides the fifth. The facts observed in these cases* can, perhaps, be only explained by the influence which the fifth nerve exercises on the nutritive processes in the organs of the special senses. It is not unreasonable to believe, that, in paralysis of the fifth nerve, their tissues may be the seats of such changes as are seen in the laxity, the vascular congestion, œdema, and other affections of the skin of the face and other tegumentary parts which also accompany the paralysis; and that these changes, which may appear unimportant when they affect external parts, are sufficient to destroy that refinement of structure by which the organs of the special senses are adapted to their functions.

According to Magendie and Longet, destruction of the eye ensues more quickly after division of the trunk of the fifth beyond the Gasserian ganglion, or after divi-

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of special sense, with the exception of that portion of the tongue which is supplied by its gustatory branch, is well illustrated by a valuable case lately recorded by Dr. Althaus.

* Two of the best cases are published, with analyses of others, by Mr. Dixon, in the Medico-Chirurgical Transactions, vol. xxviii.

sion of the ophthalmic branch, than after division of the roots of the fifth between the brain and the ganglion. Hence it would appear as if the influence on nutrition were conveyed through the filaments of the sympathetic, which join the branches of the fifth nerve at and beyond the Gasserian ganglion, rather than through the filaments of the fifth itself; and this is confirmed by experiments in which extirpation of the superior cervical ganglion of the sympathetic produced the same destructive disease of the eye that commonly follows the division of the fifth nerve.

And yet, that the filaments of the fifth nerve, as well as those of the sympathetic, may conduct such influence, appears certain from the cases, including that by Mr. Stanley, in which the source of the paralysis of the fifth nerve was near the brain, or at its very origin, before it receives any communication from the sympathetic nerve. The existence of ganglia of the sympathetic in connection with all the principal divisions of the fifth nerve where it gives off those branches which supply the organs of special sense —for example, the connection of the ophthalmic ganglion with the ophthalmic nerve at the origin of the ciliary nerves; of the spheno-palatine ganglion with the superior maxillary division, where it gives its branches to the nose and the palate; of the otic ganglion with the inferior maxillary near the giving off of filaments to the internal ear; and of the sub-maxillary ganglion with the lingual branch of the fifth—all these connections suggest that a peculiar and probably conjoint influence of the sympathetic and fifth nerves is exercised in the nutrition of the organs of the special senses; and the results of experiment and disease confirm this, by showing that the nutrition of the organs may be impaired in consequence of impairment of the power of either of the nerves.

A possible connection between the fifth nerve and the sense of sight, is shown in cases of no unfrequent occur-

rence, in which blows or other injuries implicating the frontal nerve as it passes over the brow, are followed by total blindness in the corresponding eye. The blindness appears to be the consequence of defective nutrition of the retina; for although, in some cases, it has ensued immediately, as if from concussion of the retina, yet in some it has come on gradually like slowly progressive amaurosis, and in some with inflammatory disorganisation, followed by atrophy of the whole eye.*

Physiology of the Facial Nerve.

The facial, or *portio dura* of the seventh pair of nerves, is the motor nerve of all the muscles of the face, including the platysma, but not including any of the muscles of mastication already enumerated (p. 544); it supplies, also, the parotid gland, and through the connection of its trunk with the Vidian nerve, by the petrosal nerves, some of the muscles of the soft palate, most probably the levator palati and azygos uvulæ; by its tympanic branches it supplies the stapedius and laxator tympani, and, through the otic ganglion, the tensor tympani; through the *chorda tympani* it sends branches to the submaxillary gland and to the lingualis and some other muscular fibres of the tongue; and by branches given off before it comes upon the face, it supplies the muscles of the external ear, the posterior part of the digastricus, and the stylo-hyoideus.

To the greater number of the muscles to which it is distributed it is the sole motor nerve. No pain is produced by irritating it near its origin (Valentin), and the indications of pain which are elicited when any of its branches are irritated, may be explained by the abundant communications which, in all parts of its course, it forms with sensi-

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* Such a case is recorded by Snabilie in the Nederlandsch Lancet, August, 1846.

tive nerves, whose filaments being mingled with its own are the true source of the pain.

Besides its *motor* influence, the facial is also, by means of the fibres which are supplied to the submaxillary and parotid glands, a so-called *secretory* nerve (p. 475). For through the last-named branches impressions may be conveyed which excite increased secretion of saliva. For example, if, in a dog, the submaxillary gland be exposed, and the chorda tympani be divided, it will be seen that on stimulating the distal end of the nerve by a weak electric current, the gland becomes exceedingly vascular, and saliva is secreted in largely increased amount. Under ordinary circumstances of increased secretion of saliva by the submaxillary gland, as from the presence of food in the mouth, the stimulus is conveyed by the same channel, the chorda tympani being the *efferent* nerve in a reflex action, in which the *afferent* fibres are branches of the fifth and glosso-pharyngeal nerves.

When the facial nerve is divided, or in any other way paralyzed, the loss of power in the muscles which it supplies, while proving the nature and extent of its functions, displays also the necessity of its perfection for the perfect exercise of all the organs of the special senses. Thus, in paralysis of the facial nerve, the orbicularis palpebrarum being powerless, the eye remains open through the unbalanced action of the levator palpebræ; and the conjunctiva, thus continually exposed to the air and the contact of dust, is liable to repeated inflammation, which may end in thickening and opacity of both its own tissue and that of the cornea. These changes, however, ensue much more slowly than those which follow paralysis of the fifth nerve, and never bear the same destructive character. In paralysis of the facial nerve, also, tears are apt to flow constantly over the face, apparently because of the paralysis of the tensor tarsi muscle, and the loss of the proper direction

and form of the orifices of the puncta lachrymalia. From these circumstances, the sense of sight is impaired.

The sense of hearing, also, is impaired in many cases of paralysis of the facial nerve; not only in such as are instances of simultaneous disease in the auditory nerves, but in such as may be explained by the loss of power in the muscles of the internal ear. The sense of smell is commonly at the same time impaired through the inability to draw air briskly towards the upper part of the nasal cavities, in which part alone the olfactory nerve is distributed; because, to draw the air perfectly in this direction, the action of the dilators and compressors of the nostrils should be perfect.

Lastly, the sense of taste is impaired, or may be wholly lost, in paralysis of the facial nerve, provided the source of the paralysis be in some part of the nerve between its origin and the giving off of the chorda tympani. This result, which has been observed in many instances of disease of the facial nerve in man, appears explicable only by the influence which, through the chorda tympani, it exercises on the movements of the lingualis and the adjacent muscular fibres of the tongue; and, according to some, or probably in some animals, on the movements of the stylo-glossus. We may therefore suppose that the accurate movement of these muscles in the tongue is in some way connected with the proper exercise of taste.

Together with these effects of paralysis of the facial nerve, the muscles of the face being all powerless, the countenance acquires on the paralyzed side a characteristic, vacant look, from the absence of all expression: the angle of the mouth is lower, and the paralyzed half of the mouth looks longer than that on the other side; the eye has an unmeaning stare. All these peculiarities increase, the longer the paralysis lasts; and their appearance is exaggerated when at any time the muscles of the opposite side of the face are made active in any expression, or in any of

their ordinary functions. In an attempt to blow or whistle, one side of the mouth and cheek acts properly, but the other side is motionless, or flaps loosely at the impulse of the expired air; so in trying to suck, one side only of the mouth acts; in feeding, the lips and cheek are powerless, and food lodges between the cheek and gum.

As a nerve of expression, the seventh nerve must not be considered independent of the fifth nerve, with which it forms so many communications; for, although it is through the facial nerve alone that all the muscles of the face are put into their naturally expressive actions, yet the power which the mind has of suppressing or controlling all these expressions can only be exercised by voluntary and well-educated actions directed through the facial nerve with the guidance of the knowledge of the state and position of every muscle, and this knowledge is acquired only through the fifth nerve, which confers sensibility on the muscles, and appears, for this purpose, to be more abundantly supplied to the muscles of the face than any other sensitive nerve is to those of other parts.

Physiology of the Glosso-Pharyngeal Nerve.

The glosso-pharyngeal nerves (16, fig. 151), in the enumeration of the cerebral nerves by numbers according to the position in which they leave the cranium, are considered as divisions of the *eighth pair of nerves,* in which term are included with them the pneumogastric and accessory nerves. But the union of the nerves under one term is inconvenient, although in some parts the glosso-pharyngeal and pneumogastric are so combined in their distribution that it is impossible to separate them in either anatomy or physiology.

The glosso-pharyngeal nerve appears to give filaments through its tympanic branch (Jacobson's nerve), to the fenestra ovalis, and fenestra rotunda, and the Eustachian

tube; also, to the carotid plexus, and, through the petrosal nerve, to the spheno-palatine ganglion. After communicating, either within or without the cranium, with the pneumogastric, and soon after it leaves the cranium, with the sympathetic, digastric branch of the facial, and the accessory nerve, the glosso-pharyngeal nerve parts into the two principal divisions indicated by its name, and supplies the mucous membrane of the posterior and lateral walls of the upper part of the pharynx, the Eustachian tube, the arches of the palate, the tonsils and their mucous membrane, and the tongue as far forwards as the foramen cæcum in the middle line, and to near the tip at the sides and inferior part.

Some experiments make it probable that the glosso-pharyngeal nerve contains, even at its origin, some motor fibres, together with those of common sensation and the sense of taste. Whatever motor influence, however, is conveyed directly through the branches of the glosso-pharyngeal, may be ascribed to the filaments of the pneumogastric or accessory that are mingled with it.

The experiments of Dr. John Reid, confirming those of Panizza and Longet, tend to the same conclusions; and their results probably express nearly all the truth regarding the part of the glosso-pharyngeal nerve which is distributed to the pharynx. These results were that,—1. Pain was produced when the nerve, particularly its pharyngeal branch, was irritated. 2. Irritation of the nerve before the origin of its pharyngeal, or of any of these branches, gave rise to extensive muscular motions of the throat and lower part of the face: but when the nerve was divided, these motions were excited by irritating the upper or cranial portion, while irritation of the lower end, or that in connection with the muscles, was followed by no movement; so that these motions must have depended on a reflex influence transmitted to the muscles through other nerves by the intervention of the nervous centres.

3. When the functions of the brain and medulla oblongata were arrested by poisoning the animal with prussic acid, irritation of the glosso-pharyngeal nerve, before it was joined by any branches of the pneumogastric, gave rise to no movements of the muscles of the pharynx or other parts to which it was distributed; while, on irritating the pharyngeal branch of the pneumogastric, or the glosso-pharyngeal nerve, after it had received the communicating branches just alluded to, vigorous movements of all the pharyngeal muscles and of the upper part of the œsophagus followed.

The most probable conclusion, therefore, may be that what motor influence the glosso-pharyngeal nerve may seem to exercise, is due either to the filaments of the pneumogastric or accessory that are mingled with it, or to impressions conveyed through it to the medulla oblongata, and thence reflected to muscles through motor nerves, especially the pneumogastric, accessory, and facial. Thus, the glosso-pharyngeal nerve excites, through the medium of the medulla oblongata, the actions of the muscles of deglutition. It is the chief centripetal nerve engaged in these actions; yet not the only one, for, as Dr. John Reid has shown, the acts are scarcely disturbed or retarded when both the glosso-pharyngeal nerves are divided.

But besides being thus a nerve of common sensation in the parts which it supplies, and a centripetal nerve through which impressions are conveyed to be reflected to the adjacent muscles, the glosso-pharyngeal is also a nerve of special sensation; being the gustatory nerve, or nerve of taste, in all the parts of the tongue to which it is distributed. After many discussions, the question, which is the nerve of taste?—the lingual branch of the fifth, or the glosso-pharyngeal?—may be most probably answered by stating that they are both nerves of this special function. For very numerous experiments and cases have shown that when the trunk of the fifth nerve or its lingual branch is

paralysed or divided, the sense of taste is completely lost in the superior surface of the anterior and lateral parts of the tongue. The loss is instantaneous after division of the nerve; and, therefore, cannot be ascribed to the defective nutrition of the part, though to this, perhaps, may be ascribed the more complete and general loss of the sense of taste when the whole of the fifth nerve has been paralysed.

But, on the other hand, while the loss of taste in the part of the tongue to which the lingual branch of the fifth nerve is distributed proves that to be a gustatory nerve, the fact that the sense of taste is at the same time retained in the posterior and postero-lateral parts of the tongue, and in the soft palate and its anterior arch, to which (and to some parts of which exclusively) the glosso-pharyngeal is distributed, proves that this also must be a gustatory nerve. In a female patient at St. Bartholomew's Hospital, the left lingual branch of the fifth nerve was divided in removing a portion of the lower jaw: she lost both common sensation and the sensation of taste in the tip and the anterior parts of the left half of the tongue, but retained both in all the rest of the tongue. M. Lisfranc and others have noted similar cases; and the phenomena in them are so simple and clear, that there can scarcely be any fallacy in the conclusion that the lingual branches of both the fifth and the glosso-pharyngeal nerves are gustatory nerves in the parts of the tongue which they severally supply.

This conclusion is confirmed by some experiments on animals, and, perhaps, more satisfactorily as concerns the sense of taste in man, by observation of the parts of the tongue and fauces, in which the sense is most acute. According to Valentin's experiments made on thirty students, the parts of the tongue from which the clearest sensations of taste are derived, are the base, as far as the foramen cæcum and lines diverging forwards on each side from it;

the posterior palatine arches down to the epiglottis; the tonsils and upper part of the pharynx over the root of the tongue. These are the seats of the distribution of the glosso-pharyngeal nerve. The anterior dorsal surface, and a portion of the anterior and inferior surface of the tongue, in which the lingual branch of the fifth is alone distributed, conveyed no sense of taste in the majority of the subjects of Valentin's experiments; but even if this were generally the case, it would not invalidate the conclusion that, in those who have the sense of taste in the anterior and upper part of the tongue, the lingual branch of the fifth is the nerve by which it is exercised.

Physiology of the Pneumogastric Nerve.

The *pneumogastric nerve, nervus vagus,* or *par vagum* (1, fig. 151), has, of all the cranial and spinal nerves, the most various distribution, and influences the most various functions, either through its own filaments, or those which, derived from other nerves, are mingled in its branches.

The parts supplied by the branches of the pneumogastric nerve are as follows: by its pharyngeal branches, which enter the pharyngeal plexus, a large portion of the mucous membrane, and, probably, all the muscles of the pharynx; by the superior laryngeal nerve, the mucous membrane of the under surface of the epiglottis, the glottis, and the greater part of the larynx, and the crico-thyroid muscle; by the inferior laryngeal nerve, the mucous membrane and muscular fibres of the trachea, the lower part of the pharynx and larynx, and all the muscles of the larynx except the crico-thyroid; by œsophageal branches, the mucous membrane and muscular coats of the œsophagus. Moreover, the branches of the pneumogastric nerve form a large portion of the supply of nerves to the heart and the great arteries through the cardiac nerves, derived from both the trunk and the recurrent nerve; to the lungs,

through both the anterior and the posterior pulmonary plexuses; and to the stomach, by its terminal branches passing over the walls of that organ; while branches are also distributed to the liver and to the spleen.

From the parts thus enumerated as receiving nerves from the pneumogastric, it might be assumed that this latter is a nerve of mixed function, both sensitive and motor. Experiments prove that it is so from its origin, for the irritation of its roots, even within the cranial cavity, produces both pain and convulsive movements of the larynx and pharynx; and when it is divided within the skull, the same movements follow the irritation of the distal portion, showing that they are not due to reflex action. Similar experiments prove that, through its whole course, it contains both sensitive and motor fibres, but after it has emerged from the skull, and, in some instances even sooner, it enters into so many anastomoses that it is hard to say whether the filaments it contains are, from their origin, its own, or whether they are derived from other nerves combining with it. This is particularly the case with the filaments of the sympathetic nerve, which are abundantly added to nearly all the branches of the pneumogastric. The likeness to the sympathetic which it thus acquires is further increased by its containing many filaments derived, not from the brain, but from its own petrosal ganglia, in which filaments originate, in the same manner as in the ganglia of the sympathetic, so abundantly that the trunk of the nerve is visibly larger below the ganglia than above them (Bidder and Volkmann). Next to the sympathetic nerve, that which most importantly communicates with the pneumogastric is the accessory nerve, whose internal branch joins its trunk, and is lost in it.

Properly, therefore, the pneumogastric might be regarded as a triple-mixed nerve, having out of its own sources, motor, sensitive, and sympathetic or ganglionic nerve-fibres; and to this natural complexity it adds that

which it derives from the reception of filaments from the sympathetic, accessory, and cervical nerves, and, probably, the glosso-pharyngeal and facial.

The most probable account of the particular functions which the branches of the pneumogastric nerve discharge in the several parts to which they are distributed, may be drawn from Dr. John Reid's experiments on dogs. They show that,—1. The pharyngeal branch is the principal, if not the sole motor nerve of the pharynx and soft palate, and is most probably wholly motor; a part of its motor fibres being derived from the internal branch of the accessory nerve. 2. The inferior laryngeal nerve is the motor nerve of the larynx, irritation of it producing vigorous movements of the arytenoid cartilages; while irritation of the superior laryngeal nerve gives rise to no action in any of the muscles attached to the arytenoid cartilages, but merely to contractions of the crico-thyroid muscle. 3. The superior laryngeal nerve is chiefly sensitive; the inferior, for the most part, motor; for division of the recurrent nerves puts an end to the motions of the glottis, but without lessening the sensibility of the mucous membrane; and division of the superior laryngeal nerves leaves the movements of the glottis unaffected, but deprives it of its sensibility. 4. The motions of the œsophagus are dependent on motor fibres of the pneumogastric, and are probably excited by impressions made upon sensitive fibres of the same; for irritation of its trunk excites motions of the œsophagus, which extend over the cardiac portions of the stomach; and division of the trunk paralyzes the œsophagus, which then becomes distended with the food. 5. The cardiac branches of the pneumogastric nerve are one, but not the sole channel through which the influence of the central organs and of mental emotions is transmitted to the heart. 6. The pulmonary branches form the principal, but not the sole channel by which the impressions on the mucous surface of the lungs that excite respiration,

are transmitted to the medulla oblongata. Dr. Reid was unable to determine whether they contain motor fibres.

From these results, and by referring to what has been said in former chapters, the share which the pneumogastric nerve takes in the functions of the several parts to which it sends branches, may be understood:—

1. In deglutition, the motions of the pharynx are of the reflex kind. The stimulus of the food or other substance to be swallowed, acting on the filaments of the glosso-pharyngeal nerve as well as the filaments of the superior laryngeal given to the pharynx, and of some other nerves, perhaps, with which these communicate, is conducted to the medulla oblongata, whence it is reflected, chiefly through the pneumogastric, to the muscles of the pharynx.

2. In the functions of the larynx, the sensitive filaments of the pneumogastric supply that acute sensibility by which the glottis is guarded against the ingress of foreign bodies, or of irrespirable gases. The contact of these stimulates the filaments of the superior laryngeal branch of the pneumogastric; and the impression conveyed to the medulla oblongata, whether it produce sensation or not, is reflected to the filaments of the recurrent or inferior laryngeal branch, and excites contraction of the muscles that close the glottis. Both these branches of the pneumogastric co-operate also in the production and regulation of the voice; the inferior laryngeal determining the contraction of the muscles that vary the tension of the vocal cords, and the superior laryngeal conveying to the mind the sensations of the state of these muscles necessary for their continuous guidance. And both the branches co-operate in the actions of the larynx in the ordinary slight dilatation and contraction of the glottis in the acts of expiration and inspiration, and more evidently in those of coughing and other forcible respiratory movements (p. 222).

3. It is partly through their influence on the sensibility

and muscular movements in the larynx, that the pneumogastric nerves exercise so great an influence on the respiratory process, and that the division of both the nerves is commonly fatal. To determine how death is in these cases produced, has been the object of innumerable, and often contradictory, experiments. It is probably produced differently in different cases, and in many is the result of several co-operating causes. Thus, after division of both the nerves, the respiration at once becomes slower, the number of respirations in a given time being commonly diminished to one-half, probably because the pneumogastric nerves are the principal conductors of the impression of the necessity of breathing to the medulla oblongata. Respiration does not cease; for it is probable that the impression may be conveyed to the medulla oblongata through the sensitive nerves of all parts in which the imperfectly aerated blood flows (see p. 516); yet the respiration being retarded, adds to the other injurious effects of division of the nerves.

Again, division of both pneumogastric trunks, or of both their recurrent branches, is often very quickly fatal in young animals; but in old animals the division of the recurrent nerve is not generally fatal, and that of both the pneumogastric trunks is not always fatal (J. Reid), and, when it is so, the death ensues slowly. This difference is, probably, because the yielding of the cartilages of the larynx in young animals permits the glottis to be closed by the atmospheric pressure in inspiration, and they are thus quickly suffocated unless tracheotomy be performed (Legallois). In old animals, the rigidity and prominence of the arytenoid cartilages prevent the glottis from being completely closed by the atmospheric pressure; even when all the muscles are paralyzed, a portion at its posterior part remains open, and through this the animal continues to breathe. Yet the diminution of the orifice for respiration may add to the difficulty of maintaining life.

In the case of slower death, after division of both the pneumogastric nerves, the lungs are commonly found gorged with blood, œdematous, or nearly solid, or with a kind of low pneumonia, and with their bronchial tubes full of frothy bloody fluid and mucus, changes to which, in general, the death may be proximately ascribed. These changes are due, perhaps in part, to the influence which the pneumogastric nerves exercise on the movements of the air-cells and bronchi; yet, since they are not always produced in one lung when its pneumogastric nerve is divided, they cannot be ascribed wholly to the suspension of organic nervous influence (J. Reid). Rather, they may be ascribed to the hindrance to the passage of blood through the lungs, in consequence of the diminished supply of air and the excess of carbonic acid in the air-cells and in the pulmonary capillaries (see p. 229); in part, perhaps, to paralysis of the blood-vessels, leading to congestion; and in part, also, as the experiments of Traube especially show, they appear due to the passage of food and of the various secretions of the mouth and fauces through the glottis, which, being deprived of its sensibility, is no longer stimulated or closed in consequence of their contact. He says, that if the trachea be divided and separated from the œsophagus, or if only the œsophagus be tied, so that no food or secretion from above can pass down the treachea, no degeneration of the tissue of the lungs will follow the division of the pneumogastric nerves. So that, on the whole, death after division of the pneumogastric nerves may be ascribed, when it occurs quickly in young animals, to suffocation through mechanical closure of the paralyzed glottis: and, when it occurs more slowly, to the congestion and pneumonia produced by the diminished supply of air, by paralysis of the blood-vessels, and by the passage of foreign fluids into the bronchi; and aggravated by the diminished frequency of respiration, the insensibility to the diseased state of the

lungs, the diminished aperture of the glottis, and the loss of the due nervous influence upon the process of respiration.

4. Respecting the influence of the pneumogastric nerves on the movements of the œsophagus and stomach, the secretion of gastric fluid, the sensation of hunger, absorption by the stomach, and the action of the heart,* former pages may be referred to.

Cyon and Ludwig have discovered that a remarkable power appears to be exercised on the dilatation of the blood-vessels by a small nerve which arises, in the rabbit, from the superior laryngeal branch, or from this and the trunk of the pneumogastric nerve, and after communicating with filaments of the inferior cervical ganglion proceeds to the heart. If this nerve be divided, and its upper extremity be stimulated by a weak interrupted current, an inhibitory influence is conveyed to the vaso-motor centre in the medulla oblongata (p. 576), so as to cause, by reflex action, dilatation of the principal blood-vessels, with diminution of the force and frequency of the heart's action. From the remarkable lowering of the blood-pressure in the vessels, thus produced, this branch of the vagus is called the *depressor* nerve; and it is presumed, as an afferent nerve of the heart, to be the means of conveying to the vaso-motor centre in the medulla indications of such conditions of the heart as require a lowering of the blood pressure in the vessels; as, for example, when the heart cannot, with sufficient ease, propel blood into the already too full or too tense arteries.

* See foot-note, p. 577.

Physiology of the Spinal Accessory Nerve.

In the preceding pages it is implied that all the motor influence which the pneumogastric nerves exercise, is conveyed through filaments which, from their origin, belong to them: and this is, perhaps, true. Yet a question, which has been often discussed, may still be entertained, whether a part of the motor filaments that appear to belong to the pneumogastric nerves are not given to them from the accessory nerves.

The principal branch of the accessory nerve, its external branch, supplies the sterno-mastoid and trapezius muscles; and, though pain is produced by irritating it, is composed almost exclusively of motor fibres. It might appear very probable, therefore, that the internal branch, which is added to the trunk of the pneumogastric just before the giving off of the pharyngeal branch, is also motor; and that through it the pneumogastric nerve derives part of the motor fibres which it supplies to the muscles enumerated above. And further, since the pneumogastric nerve has a ganglion just above the part at which the internal branch of the accessory nerve joins its trunk, a close analogy may seem to exist between these two nerves and the spinal nerves with their anterior and posterior roots. In this view, Arnold and several later physiologists have regarded the accessory nerve as constituting a motor root of the vagus nerve; and, although this view cannot now be maintained, yet it is very probable that the accessory nerve gives some motor filaments to the pneumogastric. For, among the experiments made on this point, many have shown that when the accessory nerve is irritated within the skull, convulsive movements ensue in some of the muscles of the larynx; all of which, as already stated, are supplied, apparently, by branches of the pneumogastric; and (which is a very significant fact) Vrolik states that in the chimpanzee the internal branch of the accessory

does not join the pneumogastric at all, but goes direct to the larynx. On the whole, therefore, although in some of the experiments no movements in the larynx followed irritation of the accessory nerve, yet it may be concluded that this nerve gives to the pneumogastric some of the motor filaments which pass, with the laryngeal branches, to the muscles of the larynx, especially to the crico-thyroid (Bernard); although it is certain that the accessory nerve does not supply *all* the motor filaments which the branches of the pneumogastric contain.

Among the roots of the accessory nerve, the lower, arising from the spinal cord, appear to be composed exclusively of motor fibres, and to be destined entirely to the trapezius and sterno-mastoid muscles; the upper fibres, arising from the medulla oblongata, contain many sensitive as well as motor fibres.

Physiology of the Hypoglossal Nerve.

The hypoglossal or ninth nerve, or *motor linguæ*, has a peculiar relation to the muscles connected with the hyoid, bone, including those of the tongue. It supplies through its descending branch (*descendens noni*), the sterno-hyoid, sterno-thyroid, and omo-hyoid; through a special branch the thyro-hyoid, and through its lingual branches the genio-hyoid, stylo-glossus, hyo-glossus, and genio-hyo-glossus and linguales. It contributes, also, to the supply of the submaxillary gland.

The function of the hypoglossal, is, probably, exclusively motor. As a motor nerve, its influence on all the muscles enumerated above is shown by their convulsions when it is irritated, and by their loss of power when it is paralysed. The effects of the paralysis of one hypoglossal nerve are, however, not very striking in the tongue. Often, in cases of hemiplegia involving the functions of the hypoglossal nerve, it is not possible to observe any

deviation in the direction of the protruded tongue; probably because the tongue is so compact and firm that the

Fig. 151.*

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* Fig. 151. View of the nerves of the eighth pair, their distribution and connections on the left side (from Sappey after Hirschfeld and Leveillé). $\frac{2}{3}$.—1, pneumogastric nerve in the neck; 2, ganglion of its trunk; 3, its union with the spinal accessory; 4, its union with the

muscles on either side, their insertion being nearly parallel to the median line, can push it straight forwards or turn it for some distance towards either side.

Physiology of the Spinal Nerves.

Little need be added to what has been already said of these nerves (pp. 493 to 495). The anterior roots of the spinal nerves are formed exclusively of motor fibres; the posterior roots exclusively of sensitive fibres.

Beyond the ganglia all the spinal nerves appear to be mixed nerves, and to contain as well sympathetic filaments.

Of the functions of the ganglia of the spinal nerves nothing very definite is known. That they are not the reflectors of any of the ascertained reflex actions through the spinal nerves, is shown by the reflex movements ceasing when the posterior roots are divided between the ganglia and the spinal cord.

PHYSIOLOGY OF THE SYMPATHETIC NERVE.

The sympathetic nerve, or sympathetic system of nerves, obtained its name from the opinion that it is the means through which are effected the several sympathies in

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hypoglossal; 5, pharyngeal branch; 6, superior laryngeal nerve; 7, external laryngeal; 8, laryngeal plexus; 9, inferior or recurrent laryngeal; 10, superior cardiac branch; 11, middle cardiac; 12, plexiform part of the nerve in the thorax; 13, posterior pulmonary plexus; 14, lingual or gustatory nerve of the inferior maxillary; 15, hypoglossal, passing into the muscles of the tongue, giving its thyro-hyoid branch, and uniting with twigs of the lingual; 16, glosso-pharyngeal nerve; 17, spinal accessory nerve, uniting by its inner branch with the pneumogastric, and by its outer, passing into the sterno-mastoid muscle; 18, second cervicle nerve: 19, third; 20, fourth; 21, origin of the phrenic nerve, 22, 23, fifth, sixth, seventh, and eighth cervical nerves, forming with the first dorsal the brachial plexus; 24, superior cervical ganglion of the sympathetic; 25, middle cervical ganglion; 26, inferior cervical ganglion united with the first dorsal ganglion; 27, 28, 29, 30, second, third, fourth, and fifth dorsal ganglia.

morbid action which distant organs manifest. It has also been called the *nervous system of organic life*, upon the supposition, now proved erroneous, that it alone, as a nervous system, influences the organic processes. Both terms are defective; but, since the title *sympathetic nerve* has the advantage of long and most general custom in its favour, and is not more inaccurate than the other, it will be here employed.

The general differences between the fibres of the cerebro-spinal and sympathetic nerves have been already stated (p. 468); and it has been said, that although such general differences exist, and are sufficiently discernible in selected filaments of each system of nerves, yet they are neither so constant, nor of such a kind, as to warrant the supposition, that the different modes of action of the two systems can be referred to the different structures of their fibres. Rather, it is probable, that the laws of conduction by the fibres are in both systems the same, and that the differences manifest in the modes of action of the systems are due to the multiplication and separation of the nervous centres of the sympathetic: ganglia, or nerve-centres, being placed in connection with the fibres of the sympathetic in nearly all parts of their course.

According to the most general view, the sympathetic system may be described as arranged in two principal divisions, each of which consists of ganglia and connecting fibres. The first division may include those ganglia which are seated on and involve the main trunks or branches of cerebral and spinal nerves. This division will include the large Gasserian ganglion on the sensitive trunk of the fifth cerebral nerve (fig. 152), the ganglia on the glosso-pharyngeal and pneumogastric nerves, and the ganglia on the posterior or sensitive branches of the spinal nerves (fig. 141).

To the second division belong the double chain of prævertebral ganglia (24 to 30, fig. 151) and their branches, extending from the interior and base of the skull to the

coccyx; the various sympathetic visceral plexuses and

Fig. 152.*

* Fig. 152. General plan of the branches of the fifth pair (after a sketch by Charles Bell). ½.—1, lesser root of the fifth pair; 2, greater root passing forwards into the Gasserian ganglion; 3, placed on the bone above the ophthalmic nerve, which is seen dividing into the supra-orbital, lachrymal, and nasal branches, the latter connected with the ophthalmic ganglion; 4, placed on the bone close to the foramen rotundum, marks the superior maxillary division, which is connected below with the spheno-palatine ganglion, and passes forwards to the infra-orbital foramen; 5, placed on the bone over the foramen ovale, marks the submaxillary nerve, giving off the anterior auricular and muscular branches, and continued by the inferior dental to the lower jaw, and by the gustatory to the tongue; *a*, the submaxillary gland, the submaxillary ganglion placed above it in connection with the gustatory nerve: 6, the chorda tympani; 7, the facial nerve issuing from the stylo-mastoid foramen.

their ganglia, as the cardiac, the solar, the renal and hypogastric plexuses; and in the same division may be included the ganglia in the neighbourhood of the head and neck, namely, the ophthalmic or lenticular, the spheno-palatine, the otic, and the submaxillary ganglia (fig. 152).

The structure of all these ganglia appears to be essentially similar, all containing—1*st*, nerve-fibres traversing them; 2*ndly*, nerve-fibres originating in them; 3*rdly*, nerve- or ganglion-corpuscles, giving origin to these fibres; and 4*thly*, other corpuscles that appear free. And in the trunk, and thence proceeding branches of the sympathetic, there appear to be always—1*st*, fibres which arise in its own ganglia; 2*ndly*, fibres derived from the ganglia of the cerebral and spinal nerves; 3*rldy*, fibres derived from the brain and spinal cord and transmitted through the roots of their nerves. The spinal cord, indeed, appears to furnish a large source of the fibres of the sympathetic nerve.

Respecting the course of the filaments belonging to the sympathetic, the following appears to have been determined. Of the filaments derived from the ganglia on the cerebral nerves, some may pass towards the brain; for, in the trunks of the nerves, between the ganglia and the brain, fine filaments like those of the sympathetic are found. But these may be proceeding from the brain to the ganglia; and, on the whole, it is probable that nearly all the filaments originating in the ganglia or cerebral nerves, go out towards the tissues and organs to be supplied, some of them being centrifugal, some centripetal; so that each ganglion with its outgoing filaments may form a kind of special nervous system appropriated to the part in which its filaments are placed. Such, for example, may be the ophthalmic ganglion with the ciliary nerves, connected with the brain and the rest of the sympathetic system by the branches of the third, fifth, and sympathetic nerves that form its roots, yet, by filaments of its

own, controlling in some mode and degree, the processes in the interior of the eye.

Of the fibres that arise in the spinal ganglia, some appear to pass into the posterior branches of the spinal nerves, and to be distributed with them; the rest pass through the branches by which the spinal nerves communicate with the trunks of the sympathetic, and then entering the sympathetic are distributed with its branches to the viscera. With these, also a certain number of the large ordinary cerebro-spinal nerve-fibres, after traversing the ganglia, pass into the sympathetic.

Of the fibres derived from the ganglia of the sympathetic itself, some go straightway towards the viscera, the rest pass through the branches of communication between the sympathetic and the branches of the spinal nerves, and joining these spinal nerves, proceed with them to their respective seats of distribution, especially to the more sensitive parts.

Thus, through these communicating branches, which have been generally called roots or origins of the sympathetic nerve, an interchange is effected between all the spinal nerves and the sympathetic trunks; all the ganglia, also, which are seated on the cerebral nerves, have roots (as they are called) through which filaments of the cerebral nerves are added to their own. So that, probably, all sympathetic nerves contain some intermingled cerebral or spinal nerve-fibres; and all cerebral and spinal nerves some filaments derived from the sympathetic system or from ganglia. But the proportions in which these filaments are mingled are not uniform. The nerves which arise from the brain and spinal cord retain throughout their course and distribution a preponderance of *cerebro-spinal* fibres, while the nerves immediately arising from the so-called sympathetic ganglia probably contain a majority of *sympathetic* fibres. But inasmuch as there is no certainty that in structure the branches of cerebral

or spinal nerves differ always from those of the sympathetic system, it is impossible in the present state of our knowledge to be sure of the source of fibres which from their structure might lead the observer to believe that they arose from the brain or spinal cord on the one hand, or from the sympathetic ganglia on the other. In other words, although the large white tubular fibres are especially characteristic of cerebro-spinal nerves, and the pale or gelatinous fibres of a sympathetic nerve, in which they largely preponderate, there is no certainty to be obtained in a doubtful case, of whether the nerve-fibre is derived from one or the other, from mere examination of its structure. It may be derived from either source.

With respect to the functions of the sympathetic nervous system, it may be stated generally that the sympathetic nerve-fibres are simple conductors of impressions, as those of the cerebro-spinal system are, and that the ganglionic centres have (each in its appropriate sphere) the like powers both of conducting and of communicating impressions. Their power of conducting impressions is sufficiently proved in ordinary diseases, as when any of the viscera, usually unfelt, give rise to sensations of pain, or when a part not commonly subject to mental influence is excited or retarded in its actions by the various conditions of the mind; for in all these cases impressions must be conducted to and fro through the whole distance between the part and the spinal cord and brain. So, also, in experiments, now more than sufficiently numerous, irritations of the semilunar ganglia, the splanchnic nerves, the thoracic, hepatic, and other ganglia and nerves, have elicited expressions of pain, and have excited movements in the muscular organs supplied from the irritated part.

In the case of pain excited, or movements affected by the mind, it may be supposed that the conduction of impressions is effected through the cerebro-spinal fibres which are mingled in all, or nearly all, parts of the sym-

pathetic nerves. There are no means of deciding this; but if it be admitted that the conduction is effected through the cerebro-spinal nerve-fibres, then, whether or not they pass uninterruptedly between the brain or spinal cord and the part affected, it must be assumed that their mode of conduction is modified by the ganglia. For, if such cerebro-spinal fibres are conducted in the ordinary manner, the parts should be always sensible and liable to the influence of the will, and impressions should be conveyed to and fro instantaneously. But this is not the case; on the contrary, through the branches of the sympathetic nerve and its ganglia, none but intense impressions, or impressions exaggerated by the morbid excitability of the nerves or ganglia, can be conveyed.

Respecting the general action of the ganglia of the sympathetic nerve, little need be said here, since they may be taken as examples by which to illustrate the common modes of action of all nerve-centres (see p. 483). Indeed, complex as the sympathetic system, taken as a whole, is, it presents in each of its parts a simplicity not to be found in the cerebro-spinal system: for each ganglion with afferent and efferent nerves forms a simple nervous system, and might serve for the illustration of all the nervous actions with which the mind is unconnected. But it will be more convenient to consider the ganglia now in connection with the functions that they may be supposed to control, in the several organs supplied by the sympathetic system alone, or in conjunction with the cerebro-spinal.

The general processes which the sympathetic appears to influence, are those of involuntary motion, secretion, and nutrition.

Many movements take place involuntarily in parts supplied with cerebro-spinal nerves, as the respiratory and other spinal reflex motions; but the parts principally supplied with sympathetic nerves are usually capable of

none but involuntary movements, and when the mind acts on them at all, it is only through the strong excitement or depressing influence of some passion, or through some voluntary movement with which the actions of the involuntary part are commonly associated. The heart, stomach, and intestines are examples of these statements; for the heart and stomach, though supplied in large measure from the pneumogastric nerves, yet probably derive through them few filaments except such as have arisen from their ganglia, and are therefore of the nature of sympathetic fibres.

The parts which are supplied with motor power by the sympathetic nerve continue to move, though more feebly than before, when they are separated from their natural connections with the rest of the sympathetic system, and wholly removed from the body. Thus, the heart, after it is taken from the body, continues to beat in Mammalia for one or two minutes, in reptiles and Amphibia for hours; and the peristaltic motions of the intestine continue under the same circumstances. Hence the motion of the parts supplied with nerves from the sympathetic are shown to be, in a measure, independent of the brain and spinal cord.

It seems to be a general rule, at least in animals that have both cerebro-spinal and sympathetic nerves much developed, that the involuntary movements excited by stimuli conveyed through ganglia are orderly and like natural movements, while those excited through nerves without ganglia are convulsive and disorderly; and the probability is that, in the natural state, it is through the same ganglia that natural stimuli, impressing centripetal nerves, are reflected through centrifugal nerves to the involuntary muscles. As the muscles of respiration are maintained in uniform rhythmic action chiefly by the reflecting and combining power of the medulla oblongata, so, probably, are those of the heart, stomach, and intestines, by their

several ganglia. And as with the ganglia of the sympathetic and their nerves, so with the medulla oblongata and its nerves distributed to respiratory muscles,—if these nerves or the medulla oblongata itself be directly stimulated, the movements that follow are convulsive and disorderly; but if the medulla be stimulated through a centripetal nerve, as when cold is applied to the skin, then the impressions are reflected so as to produce movements which, though they may be very quick and almost convulsive, are yet combined in the plan of the proper respiratory acts.

Among the ganglia of the sympathetic nerves to which this co-ordination of movements is to be ascribed, must be reckoned, not those alone which are on the principal trunks and branches of the sympathetic external to any organ, but those also which lie in the very substance of the organs; such as those discovered in the heart by Remak. Those also may be included which have been found in the mesentery close by the intestines, as well as in the submucous tissue of the stomach and intestinal canal (Meissner), and in other parts. The extension of discoveries of such ganglia will probably diminish yet further the number of instances in which the involuntary movements appear to be effected independently of central nervous influence.

Respecting the influence of the sympathetic nerve in nutrition and secretion, we may refer to the chapters on those processes.

The influence of the sympathetic nerves on the blood-vessels has been already referred to in the Section on the Arteries. It was stated that the muscular tissue of the blood-vessels was supplied by sympathetic nerve-branches, called from their distribution and function *vaso-motor* nerves; and that by these the condition of the vessels with respect to contraction or relaxation, and therefore to the stream of blood which flowed through them in a given

time, is governed. When these vaso-motor nerves are intact, the muscular tissue of the arteries is always in a state of tonic contraction, which varies in degree at different times. When they are divided, the muscular fibres in which they are distributed are paralyzed, and the blood-vessels become dilated. The most usual experiment in illustration of these facts is performed by exposing in a rabbit the cervical sympathetic, from which vaso-motor branches are given to the blood-vessels of the head and neck. On dividing the nerve, the blood-vessels of the same side are paralyzed, and the stream of blood, now uncontrolled, dilates them. The effect is best seen in the ear, the blood-vessels of which become manifestly larger than those of the opposite side; while the part becomes redder and warmer from the increased quantity of blood circulating through it. On galvanizing the upper divided extremity of the nerve, the muscular fibres of the blood-vessels respond to the stimulus by again contracting, and the parts become paler, colder, and less sensitive than natural.

The vaso-motor nerves arise directly from the sympathetic. Thus the blood-vessels of the head and neck are supplied by branches from the superior cervical ganglion, those of the thorax from the cervical and upper dorsal ganglia, those of the abdomen chiefly by the splanchnic nerves, and so forth. But it is now generally agreed, from the results of experiments by Ludwig and others, that the principal *vaso-motor nerve-centre*, with which all these nerves communicate, and by which their action is regulated, is situate in the medulla oblongata—or, in other words, that the vaso-motor fibres, arising from this nerve-centre, pass down the spinal cord, and issuing by the anterior roots of the spinal nerves, enter the various ganglia on the præ-vertebral cord of the sympathetic, and thence reach their destination, probably taking with them fibres which arise in the ganglia through which they pass. The vaso-motor centre in the medulla appears to have a regulating power

over the whole of the vaso-motor nerves; but it seems likely that other secondary vaso-motor centres may exist in ganglia in different parts of the body, and may be the centres by which, under ordinary circumstances, vaso-motor changes are regulated in the territory in which they are placed.

The vaso-motor nerve-centres are not only centres from which influences are directly transmitted to the blood-vessels, but, like other nerve-centres, may be the means by which impulses are *reflected* (p. 486). And reflex actions occur in connection with the muscular fibres of blood-vessels, as with those of the voluntary muscles. Such reflected impressions may lead either to *contraction* or to *dilatation* of blood-vessels; or, in other words, the action may be *excito-vaso-motor*, or *vaso-inhibitory*. The most remarkable instance at present known of a nerve, the stimulation of which leads by reflex action through the vaso-motor centre in the medulla oblongata, to dilatation of blood-vessels, is the depressor branch of the vagus (p. 563); but similar effects have been observed in a less degree, on stimulating other afferent spinal nerves.*

It is, of course, very difficult to determine the relative share exercised by the true sympathetic and the ordinary cerebro-spinal fibres in the contraction of blood-vessels, and in the general processes of nutrition and secretion, since both kinds of fibres appear to be distributed to most parts, and there seems to be no possibility of isolating them. Probably the safest view of the question at present is, still to regard all the processes of organic life, in man, as liable to the combined influences of the cerebro-spinal and the sympathetic systems; to consider that those influences may be so combined as that the sympa-

* For an admirable summary of what is at present known regarding the Innervation of the Heart and Blood-vessels, see Lectures by Dr. Rutherford, in the "Lancet," December 16th, 1871, and January 20, 1872.

thetic nerves and ganglia may be in man, as in the lower animals, the parts through which the ordinary and constant influence of nervous force is exercised on the organic processes; while the cerebro-spinal nervous centres and their ganglia are so closely connected with the proper sympathetic ganglia, that neither of them can be said to be independent of the other; each, as a rule, and under ordinary circumstances, governing its own domain, but always liable to be influenced by the other.

CHAPTER XVII.

CAUSES AND PHENOMENA OF MOTION.

The most evident *vital* motions observable in the bodies of animals, are performed in one or other of the following ways: first, by means of the oscillatory motion or vibration of microscopic cilia, with which the surfaces of certain membranes are beset; and secondly, by the contraction of fibres which either have a longitudinal direction and are fixed at both extremities, or form circular bands: the contraction or shortening of the fibres bringing the parts to which they are fixed nearer to each other. There are, besides, various molecular movements allied to those which need not here be considered.

CILIARY MOTION.

Ciliary motion consists in the incessant vibration of fine, pellucid, blunt processes, about $\frac{1}{5000}$ of an inch long, termed cilia (figs. 153, 154), situated on the free extremities of the cells of epithelium covering certain surfaces of the body.

The distribution and structure of ciliary epithelium and the microscopic appearances of cilia in motion have been already described (p. 33).

Ciliary motion seems to be alike independent of the will, of the direct influence of the nervous system, and of muscular contraction, for it is involuntary; there is no nervous or muscular tissue in the immediate neighbourhood of the cilia, and it continues for several hours after death or removal from the body, provided the portion of tissue under examination be kept moist. Its independence of the nervous system is shown also in its occurrence in

Fig. 153.*

Fig. 154.†

the lowest invertebrate animals apparently unprovided with anything analogous to a nervous system, in its persistence in animals killed by prussic acid, by narcotic or other poisons, and after the direct application of narcotics to the ciliary surface, or the discharge of a Leyden jar, or of a galvanic shock through it. The vapour of chloroform arrests the motion; but it is renewed on the discontinuance of the application (Lister). According to Kuhne, the movement ceases in an atmosphere deprived of oxygen, but is revived on the admission of this gas. Carbonic acid stops the movement. The contact of various substances will stop the motion altogether; but this seems to depend chiefly on destruction of the delicate substance of which the cilia are composed.

Little or nothing is known with certainty regarding the nature of ciliary action. As Dr. Sharpey observes,

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* Fig. 153. Spheroidal ciliated cells from the mouth of the frog; magnified 300 diameters (Sharpey).

† Fig. 154. Columnar ciliated epithelium cells from the human nasal membrane; magnified 300 diameters (Sharpey).

however, it is a special manifestation of a similar property to that by which the other motions of animals are effected namely, by what we term *vital contractility*. The fact of the more evident movements of the larger animals being effected by a structure apparently different from that of cilia, is no argument against such a supposition. For, if we consider the matter, it will be plain that our prejudices against admitting a relationship to exist between the two structures, muscles and cilia, rests on no definite ground; and for the simple reason, that we know so little of the manner of production of movement in either case. The mere difference of structure is not an argument in point; neither is the presence or absence of nerves. The movements of both muscles and cilia are manifestations of *force*, by certain special structures, which we call respectively muscles and cilia. We know nothing more about the means by which the manifestation is effected by one of these structures than by the other; and the mere fact that one has nerves and the other has not, is no more argument against cilia having what we call a vital power of contraction, than the presence or absence of stripes from voluntary or involuntary muscles respectively, is an argument for or against the contraction of one of them being vital and the other not so. Inasmuch then as cilia are found in living structures only, and inasmuch as they are a means whereby force is transformed (see Chap. II.), their peculiar properties have as much right to be invested with the term *vital* as have those of muscular fibres. The term may be in both instances a bad one,—it certainly is an unsatisfactory one,—but it is as good for one case as the other.

MUSCULAR MOTION.

There are two chief kinds of muscular tissue, the *striped*, and the *plain* or *unstriped*, and they are distinguished by structural peculiarities and mode of action. The striped form of muscular fibre is sometimes called *voluntary* muscle,

because all muscles under the control of the will are constructed of it. The plain or unstriped variety is often termed *involuntary*, because it alone is found in the greater number of the muscles over which the will has no power.

The involuntary or unstriped muscles are made up, according to Kölliker, of elongated, spindle-shaped, nucleated *fibre-cells* (fig. 155), which in their most perfect form are flat, from about $\frac{1}{4500}$ to $\frac{1}{3500}$ of an inch broad, and about $\frac{1}{600}$ to $\frac{1}{300}$ of an inch in length,—very clear, granular, and brittle, so that when they break, they often have abruptly rounded or square extremities. Each fibre-

Fig. 155.*

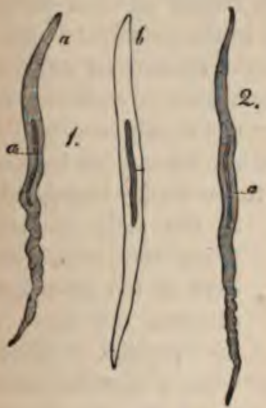


Fig. 156.†

cell possesses an elongated nucleus, and many are marked along the middle, or, more rarely, along one of the edges,

* Fig. 155. Muscular fibre-cells from human arteries, magnified 350 diameters (Kölliker). *a*, natural state; *b*, treated with acetic acid.

† Fig. 156. Plain muscular fibres from the human bladder, magnified 250 diameters. *a*, in their natural state; *b*, treated with acetic acid to show the nuclei.

either by a fine continuous dark streak, or by short isolated dark lines, or by dark points arranged in a row, or scattered. These fibre-cells, by their union, form *fibres* and bundles of fibres (fig. 156). The fibres have no distinct sheath.

The fibres of involuntary muscle, such as are here described, form the proper muscular coats of the digestive canal from the middle of the œsophagus to the internal sphincter ani, of the ureters and urinary bladder, the trachea and bronchi, the ducts of glands, the gall-bladder, the vesiculæ seminales, the pregnant uterus, of blood-vessels and lymphatics, the iris, and some other parts.

This form of tissue also enters largely into the composition of the tunica dartos, and is the principal cause of the wrinkling and contraction of the scrotum on exposure to cold. The fibres of the cremaster assist in some measure in producing this effect, but they are chiefly concerned in drawing up the testis and its coverings towards the inguinal opening. Unstriped muscular tissue occurs largely also in the cutis (p. 421), being especially abundant at the interspaces between the bases of the papillæ. Hence, when it contracts under the influence of cold, fear, electricity, or any other stimulus, the papillæ are made unusually prominent, and give rise to the peculiar rough-

Fig. 157.*

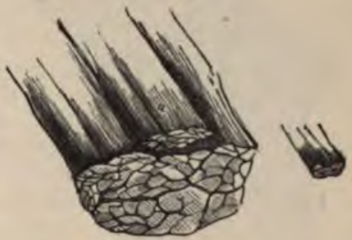
* Fig. 157. Perpendicular section through the scalp, with two hair-sacs; *a*, epidermis: *b*, cutis, *c*, muscles of the hair-follicles (after Kölliker).

ness of the skin termed *cutis anserina*, or goose-skin. It occurs also in the superficial portion of the cutis, in all parts where hairs occur, in the form of flattened roundish bundles, which lie alongside the hair-follicles and sebaceous glands. They pass obliquely from without inwards, embrace the sebaceous glands, and are attached to the hair follicles near their base (fig. 157).

To this kind of muscular fibre the term *organic* is often applied, from the fact that it enters especially into the construction of such parts as are concerned in what has been called *organic* life (see note, p. 464).

The muscles of *animal* life, or *striped* muscles, include the whole class of *voluntary* muscles, the *heart*, and those muscles neither completely voluntary nor involuntary, which form part of the walls of the pharynx, and exist in many other parts of the body, as the internal ear, urethra, etc. All these muscles are composed of fleshy bundles called *fasciculi*, enclosed in coverings of fibro-cellular tissue, by which each is at once connected with, and isolated from, those adjacent to it (fig. 158). Each bundle is again divided into smaller ones, similarly ensheathed and similarly divisible; and so on, through an uncertain number of gradations, till one arrives at the *primitive* fasciculi, or the muscular *fibres* peculiarly so called.

Fig. 158.*



* Fig. 158. A small portion of muscle, natural size, consisting of larger and smaller fasciculi, seen in a transverse section, and the same magnified 5 diameters (after Sharpey).

Muscular *fibres* consist, each of them, of a tube or sheath of delicate structureless membrane, called the *sarcolemma*, enclosing a number of filaments or *fibrils*. They are cylindriform or prismatic, with five or more sides, according to the manner in which they are compressed by adjacent fibres. Their average diameter is about $\frac{1}{500}$ of an inch, and their length never exceeds an inch and a half.

Fig. 159.*

Each muscular fibre is thus constructed :—Externally is a fine, transparent, structureless membrane, called the *sarcolemma*, which in the form of a tubular investing sheath forms the outer wall of the fibre, and is filled by the contractile material of which the fibre is chiefly made up. Sometimes, from its comparative toughness, the sarcolemma will remain untorn, when by extension the contained part can be broken (fig. 159), and its presence is in this way best demonstrated. The fibres, which are cylindriform or prismatic, with an average diameter of about $\frac{1}{500}$ of an inch, are of a pale yellow colour, and apparently marked by fine striæ, which pass transversely

Fig. 160.†

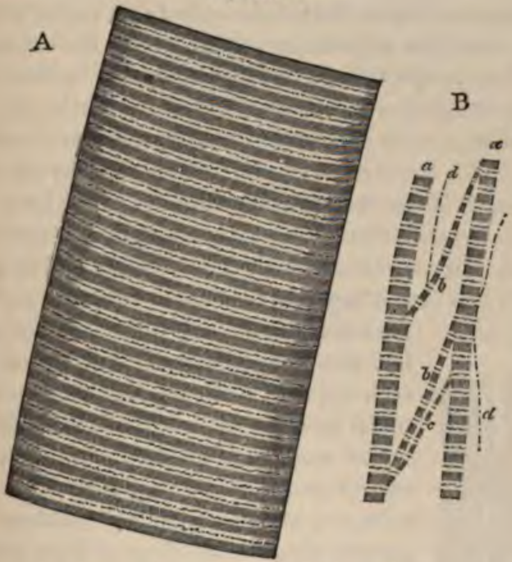
* Fig. 159. Muscular fibre torn across ; the sarcolemma still connecting the two parts of the fibre (after Todd and Bowman).

† Fig. 160. A few muscular fibres, being part of a small fasciculus, highly magnified, showing the transverse striæ. *a*, end view of *b*, *b*, bres ; *c*, a fibre split into its fibrils (after Sharpey).

round them, in slightly curved or wholly parallel lines. Other, but generally more obscure striæ, also pass longitudinally over the tubes, and indicate the direction of the filaments or primitive *fibrils* of which the substance of each *fibre* is composed (fig. 160).

The whole substance of the fibre contained within the sarcolemma may be thus supposed to be constructed of longitudinal fibrils—a bundle of *fibrils* surrounded by the sarcolemma constituting a *fibre*.

Fig. 161.*



There is still some doubt regarding the nature of the fibrils. Each of them appears to be composed of a single row of minute dark quadrangular particles called sarcous

* Fig. 161. A. Portion of a medium-sized human muscular fibre, magnified nearly 800 diameters. B. *Separated bundles of fibrils* equally magnified; *a*, *a*, larger, and *b*, *b*, smaller collections; *c*, still smaller; *d*, *d*, the smallest which could be detached, possibly representing a single series of sarcous elements (after Sharpey).

elements, which are separated from each other by a bright space formed of a pellucid substance continuous with them. A fine streak can be sometimes discerned passing across the bright interval between the sarcous elements. Dr. Sharpey believes that, even in a fibril so constituted, the ultimate anatomical element of the fibre has not been isolated. He believes that each fibril with quadrangular sarcous elements is composed of a number of other fibrils still finer, so that the sarcous element of an ultimate fibril would be not quadrangular but as a streak, and the dark transverse streak on the bright space but a row of dots. In either case the appearance of striation in the whole fibre would be produced by the arrangement, side by side, of the dark and light portions respectively of the fibrils (fig. 161).

Although each muscular fibre may be considered to be formed of a number of longitudinal fibrils, arranged side by side, it is also true that they are not naturally separate from each other, there being lateral cohesion, if not fusion, of each sarcous element with those around and in contact with it; so that it happens that there is a tendency for a fibre to split, not only into separate fibrils, but also occasionally into plates or disks, each of which is composed of sarcous elements laterally adherent one to another.

Fig. 162.*

The muscular fibres of the heart, although striped and resembling closely those of the voluntary muscles in their general structure, present these distinctions:—They are finer and more faintly striated, they branch and anastomose one with another, and no sarcolemma can be usually discerned (fig 162).

The voluntary muscles are freely supplied with blood-vessels; the capillaries form a network with oblong meshes

* Fig. 162. Muscular fibres from the heart, magnified, showing their cross-striæ, divisions and junctions (from Kölliker).

around the fibres on the outside of the sarcolemma. No vessels penetrate the sarcolemma to enter the interior of the fibre.

Nerves also are supplied freely to muscles; the voluntary muscles receiving chiefly nerves from the cerebrospinal system, and the unstriped muscles from the sympathetic or ganglionic system.

Properties of Muscular Tissue.

The property of muscular tissue, by which its peculiar functions are exercised, is its contractility, which, in the contraction or shortening of muscle, is excited by all kinds of stimuli, applied either directly to the muscles, or indirectly to them through the medium of their motor nerves. This property, although commonly brought into action through the nervous system, is inherent in the muscular tissue. For—1*st*, it may be manifested in a muscle which is isolated from the influence of the nervous system by division of the nerves supplying it, so long as the natural tissue of the muscle is duly nourished; and 2*ndly*, it is manifest in a portion of muscular fibre, in which, under the microscope, no nerve-fibre can be traced.

If the removal of nervous influence be long continued, as by division of the nerve supplying a muscle, or in cases of paralysis of long-standing, the irritability, *i.e.*, the power of both perceiving and responding to a stimulus, may be lost; but probably this is chiefly due to the impaired nutrition of the muscular tissue, which ensues through its inaction (J. Reid). The irritability of muscles is also of course soon lost, unless a supply of arterial blood to them is kept up. Thus, after ligature of the main arterial trunk of a limb, the power of moving the muscles is partially or wholly lost, until the collateral circulation is established; and when, in animals, the abdominal aorta is tied, the hind legs are rendered almost powerless (Segalas). So, also, it is to the imperfect supply of arterial blood to

the muscular tissue of the heart, that the cessation of the action of this organ in asphyxia is in some measure due (p. 231).

Besides the property of contractility, the muscles, especially the *striated* or those of *animal* life, possess sensibility by means of the sensitive nerve-fibres distributed to them. The amount of common sensibility in muscles is not great; for they may be cut or pricked without giving rise to severe pain, at least in their healthy condition. But they have a peculiar sensibility, or at least a peculiar modification of common sensibility, which is shown in that their nerves can communicate to the mind an accurate knowledge of their states and positions when in action. By this sensibility, we are not only made conscious of the morbid sensations of fatigue and cramp in muscles, but acquire, through muscular action, a knowledge of the distance of bodies and their relation to each other, and are enabled to estimate and compare their weight and resistance by the effort of which we are conscious in measuring, moving, or raising them. Except with such knowledge of the position and state of each muscle, we could not tell how or when to move it for any required action; nor without such a sensation of effort could we maintain the muscles in contraction for any prolonged exertion.

The *mode of contraction* in the transversely-striated muscular tissue, has been much disputed. The most probable account, which has been especially illustrated by Mr. Bowman, is that the contraction is effected by an approximation of the constituent parts of the fibrils, which, at the instant of contraction, without any alteration in their general direction, become closer, flatter, and wider; a condition which is rendered evident by the approximation of the transverse striæ seen on the surface of the fasciculus, and by its increased breadth and thickness. The appearance of the zigzag lines into which it was supposed the fibres are thrown in contraction, is due to the relaxation of

a fibre which has been recently contracted, and is not at once stretched again by some antagonist fibre, or whose extremities are kept close together by the contractions of other fibres. The contraction is therefore a simple, and, according to Ed. Weber, an uniform, simultaneous, and steady shortening of each fibre and its contents. What each fibril or fibre loses in length, it gains in thickness: the contraction is a change of form not of size; it is, therefore, not attended with any diminution in bulk, from condensation of the tissue. This has been proved for entire muscles, by making a mass of muscle, or many fibres together, contract in a vessel full of water, with which a fine, perpendicular, graduated tube communicates. Any diminution of the bulk of the contracting muscle would be attended by a fall of fluid in the tube; but when the experiment is carefully performed, the level of the water in the tube remains the same, whether the muscle be contracted or not.*

In thus shortening, muscles appear to swell up, becoming rounder, more prominent, harder, and apparently tougher. But this hardness of muscle in the state of contraction, is not due to increased firmness or condensation of the muscular tissue, but to the increased tension to which the fibres, as well as their tendons and other tissues, are subjected from the resistance ordinarily opposed to their contraction. When no resistance is offered, as when a muscle is cut off from its tendon, not only is no hardness perceived during contraction, but the muscular tissue is even softer, more extensile, and less elastic than in its ordinary uncontracted state (Ed. Weber).

Heat is developed in the contraction of muscles. Becquerel and Breschet found, with the thermo-multiplier,

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* Edward Weber, however, states that a very slight diminution does take place in the bulk of a contracting muscle; but it is so slight as to be practically of no moment.

about 1° of heat produced by each forcible contraction of a man's biceps; and when the actions were long continued, the temperature of the muscle increased 2°. It is not known whether this development of heat is due to chemical changes ensuing in the muscle, or to the friction of its fibres vigorously acting: in either case, we may refer to it a part of the heat developed in active exercise (p. 233). And Nasse suspects that to it is due the higher temperature of the blood in the left ventricle; for he says that this fluid is always warmer in the left ventricle than in the left auricle, and that the blood in the latter is but little warmer than that on the right side of the heart. But these experiments need confirmation.

Sound is said to be produced when muscles contract forcibly. Dr. Wollaston showed that this sound might be easily heard by placing the tip of the little finger in the ear, and then making some muscles contract, as those of the ball of the thumb, whose sound may be conducted to the ear through the substance of the hand and finger. A low shaking or rumbling sound is heard, the height and loudness of the note being in direct proportion to the force and quickness of the muscular action, and to the number of fibres that act together, or, as it were, in time.

The two kinds of fibres, the striped and unstriped, have characteristic differences in the mode in which they act on the application of the same stimulus; differences which may be ascribed in great part to their respective differences of structure, but to some degree possibly, to their respective modes of connection with the nervous system. When irritation is applied directly to a muscle with striated fibres, or to the motor nerve supplying it, contraction of the part irritated, and of that only, ensues; and this contraction is instantaneous, and ceases on the instant of withdrawing the irritation. But, when any part with unstriped muscular fibres, *e.g.*, the intestines or bladder, is

irritated, the subsequent contraction ensues more slowly, extends beyond the part irritated, and with alternating relaxation, continues for some time after the withdrawal of the irritation. Ed. Weber particularly illustrated the difference in the modes of contraction of the two kinds of muscular fibres by the effects of the electro-magnetic stimulus. The rapidly succeeding shocks given by this means to the nerves of muscles excite in all the transversely-striated muscles a fixed state of tetanic contraction, which lasts as long as the stimulus is continued, and on its withdrawal instantly ceases: but in the muscles with smooth fibres they excite, if any movement, only one that ensues slowly, is comparatively slight, alternates with rest, and continues for a time after the stimulus is withdrawn.

In their mode of responding to these stimuli, all the voluntary muscles, or those with transverse striæ, are alike; but among those with plain or unstriped fibres there are many differences,—a fact which tends to confirm the opinion that their peculiarity depends as well on their connection with nerves and ganglia as on their own properties. According to Weber, the ureters and gall-bladder are the parts least excited by stimuli: they do not act at all till the stimulus has been long applied, and then contract feebly, and to a small extent. The contractions of the cæcum and stomach are quicker and wider-spread: still quicker those of the iris, and of the urinary bladder if it be not too full. The actions of the small and large intestines, of the vas deferens, and pregnant uterus, are yet more vivid, more regular, and more sustained; and they require no more stimulus than that of the air to excite them. The heart is the quickest and most vigorous of all the muscles of organic life in contracting upon irritation, and appears in this, as in nearly all other respects, to be the connecting member of the two classes of muscles.

All the muscles retain their property of contracting under the influence of stimuli applied to them or to their

nerves for some time after death, the period being longer in cold-blooded than in warm-blooded Vertebrata, and shorter in birds than in Mammalia. It would seem as if the more active the respiratory process in the living animal, the shorter is the time of duration of the irritability in the muscles after death; and this is confirmed by the comparison of different species in the same order of Vertebrata. But the period during which this irritability lasts, is not the same in all persons, nor in all the muscles of the same persons. In a man it ceases, according to Nysten, in the following order:—first in the left ventricle, then in the intestines and stomach, the urinary bladder, right ventricle, œsophagus, iris; then in the voluntary muscles of the trunk, lower and upper extremities; lastly in the right and left auricle of the heart.

After the muscles of the dead body have lost their irritability or capability of being excited to contraction by the application of a stimulus, they spontaneously pass into a state of contraction, apparently identical with that which ensues during life.* It affects all the muscles of the body; and, where external circumstances do not prevent it, commonly fixes the limbs in that which is their natural posture of equilibrium or rest. Hence, and from the simultaneous contraction of all the muscles of the trunk, is produced a general stiffening of the body, constituting the *rigor mortis* or *post-mortem rigidity*.†

* If, however, arterial blood be made to circulate through the body or through a limb, the *post mortem* contraction of the muscles thus supplied with blood, may, as Dr. Brown-Séquard has shown, be suspended, and the muscles again admit of contracting on the application of a stimulus.

† It should be stated here, however, that the generally accepted explanation of the state of the muscles during *rigor mortis*, namely, that it is due to contraction of the fibres, as in strong action during life, is denied by some physiologists, who maintain that the condition of the muscles is not due to contraction at all, but is caused by a kind of coagulation of the inter-fibrillar juices. This idea has been of late especially supported by r. Norris (see Camb. J. of Anat. and Phys., Part I.).

The muscles are not affected exactly simultaneously by the *post-mortem* contraction, but rather in succession. It affects the neck and lower jaw first; next, the upper extremities, extending from above downwards; and lastly, reaches the lower limbs; in some rare instances only, it affects the lower extremities before, or simultaneously with, the upper extremities. It usually ceases in the order in which it began; first at the head, then in the upper extremities, and lastly in the lower extremities. According to Sommer, it never commences earlier than ten minutes, and never later than seven hours, after death; and its duration is greater in proportion to the lateness of its accession. According to Schiffer, and others have confirmed the truth of his observation, heat is developed during the passage of a muscular fibre into the condition of rigor mortis.

Since rigidity does not ensue until muscles have lost the capacity of being excited by external stimuli, it follows that all circumstances which cause a speedy exhaustion of muscular irritability, induce an early occurrence of the rigidity, while conditions by which the disappearance of the irritability is delayed, are succeeded by a tardy onset of this rigidity. Hence its speedy occurrence, and equally speedy departure in the bodies of persons exhausted by chronic diseases; and its tardy onset and long continuance after sudden death from acute diseases. In some cases of sudden death from lightning, violent injuries, or paroxysms of passion, rigor mortis has been said not to occur at all; but this is not always the case. It may, indeed, be doubted whether there is really a complete absence of the post-mortem rigidity in any such cases; for the experiments of M. Brown-Séquard with electro-magnetism make it probable that the rigidity may supervene immediately after death, and then pass away with such rapidity as to be scarcely observable. Thus, he took five rabbits, and killed them by removing their hearts. In the first, rigidity

came on in 10 hours, and lasted 192 hours; in the second, which was feebly electrified, it commenced in seven hours, and lasted 144; in the third, which was more strongly electrified, it came on in two, and lasted 72 hours; in the fourth, which was still more strongly electrified, it came on in one hour, and lasted 20; while, in the last rabbit, which was submitted to a powerful electro-galvanic current, the rigidity ensued in seven minutes after death, and passed away in 25 minutes. From this it appears that the more powerful the electric current, the sooner does the rigidity ensue, and the shorter is its duration; and as the lightning shock is so much more powerful than any ordinary electric discharge, the rigidity may ensue so early after death and pass away so rapidly as to escape detection. The influence exercised upon the onset and duration of post-mortem rigidity by causes which exhaust the irritability of the muscles, was well illustrated in further experiments by the same physiologist, in which he found that the rigor mortis ensued far more rapidly, and lasted for a shorter period in those muscles which had been powerfully electrified just before death than in those which had not been thus acted upon.

The occurrence of rigor mortis is not prevented by the previous existence of paralysis in a part, provided the paralysis has not been attended with very imperfect nutrition of the muscular tissue.

The rigidity affects the involuntary as well as the voluntary muscles, whether they be constructed of striped or unstriped fibres. The rigidity of involuntary muscles with striped fibres is shown in the contraction of the heart after death. The contraction of the muscles with unstriped fibres is shown by an experiment of Valentin, who found that if a graduated tube connected with a portion of intestine taken from a recently-slain animal, be filled with water, and tied at the opposite end, the water will in a few hours rise to a considerable height in the tube,

owing to the contraction of the intestinal walls. It is still better shown in the arteries, of which all that have muscular coats contract after death, and thus present the roundness and cord-like feel of the arteries of a limb lately removed, or those of a body recently dead. Subsequently they relax, as do all the other muscles, and feel lax and flabby, and lie as if flattened, and with their walls nearly in contact.*

Actions of the Voluntary Muscles.

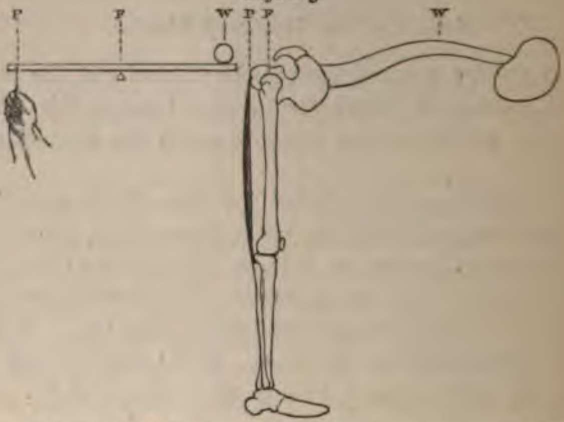
The greater part of the voluntary muscles of the body act as sources of power for moving levers,—the latter consisting of the various bones to which the muscles are attached.

All levers have been divided into three kinds, according to the relative position of the *power*, the *weight* to be moved, and the *axis of motion* or *fulcrum*. In a lever of the *first* kind the *power* is at one extremity of the lever, the *weight* at the other, and the *fulcrum* between the two. If the initial letters only of the *power*, *weight*, and *fulcrum* be used, the arrangement will stand thus:—P.F.W. A

* Although the preceding remarks represent the views generally entertained in regard to muscular action, yet it must be observed that a new and very different theory on the subject has been lately advanced by several writers, and especially developed by Dr. Radcliffe, who has also made it the basis of new views on the pathology of various convulsive affections. According to this doctrine, the ordinary relaxed or elongated state of a muscle is due to a certain "state of polarity" in which the muscle is maintained, and contraction is brought about by anything (such as an effort of the will) which liberates the muscle from this influence, and thus leaves it to the operation of the attractive force inherent in the muscular molecules. According to this doctrine, also, the stage of rigor mortis is readily explicable: death depriving the muscles of the "state of polarity" whereby they had hitherto been kept relaxed, and thus allowing the attractive force of the muscular particles to come into play. For facts and arguments in support of this view, and for references and confirmatory opinions, Dr. Radcliffe's work On Epileptic and other Convulsive Affections may be consulted.

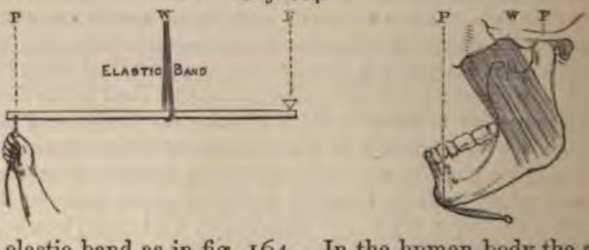
poker, as ordinarily used, or the bar in fig. 164, may be cited as an example of this variety of lever; while, as an instance in which the bones of the human skeleton are used as a lever of the same kind, may be mentioned the act of raising the body from the stooping posture by means of the hamstring muscles attached to the tuberosity of the ischium (fig. 163).

Fig. 163.



In a lever of the second kind, the arrangement is thus: —P.W.F.; and this leverage is employed in the act of raising the handles of a wheelbarrow, or in stretching

Fig. 164.



an elastic band as in fig. 164. In the human body the act of opening the mouth by depressing the lower jaw, is an example of the same kind,—the tension of the muscles which close the jaw representing the weight (fig. 164).

In a lever of the third kind the arrangement is—F.P.W., and the act of raising a pole, as in fig. 165, is an example. In the human body there are numerous examples of the employment of this kind of leverage. The act of bending the fore-arm may be mentioned as an instance (fig. 165).

Fig. 165.*

In the human body, levers are most frequently used at a disadvantage as regards power, the latter being sacrificed for the sake of a greater range of motion. Thus in the diagrams of the first and third kinds it is evident that the power is so close to the fulcrum, that great force must be exercised in order to produce motion. It is also evident, however, from the same diagrams, that by the closeness of the power to the fulcrum a great range of movement can be obtained by means of a comparatively slight shortening of the muscular fibres.

The greater number of the more important muscular actions of the human body—those, namely, which are arranged harmoniously so as to subserve some definite purpose or other in the animal economy—are described in various parts of this work, in the sections which treat of the physiology of the processes by which these muscular actions are resisted or carried out. The combined action of the respiratory muscles, for instance, will be found described in the chapter on "Respiration"; the action of the heart and blood-vessels, under the head of "Circulation"; while the movements of the stomach and intestines

are too intimately associated with the function of "Digestion," to be described apart from it. There are, however, one or two very important and somewhat complicated muscular acts which may be best described in this place.

Walking.—In the act of walking, almost every voluntary muscle in the body is brought into play, either directly for purposes of progression, or indirectly for the proper balancing of the head and trunk. The muscles of the arms are least concerned; but even these are for the most part instinctively in action also to some extent.

Among the chief muscles engaged directly in the act of walking are those of the calf, which, by pulling up the heel, pull up also the astragalus, and with it, of course, the whole body, the weight of which is transmitted through the tibia to this bone (fig. 166). When starting to walk,

Fig. 166.

1 2 3 4 5

say with the left leg, this raising of the body is not left entirely to the muscles of the left calf, but the trunk is thrown forward in such a way that it would fall prostrate were it not that the right foot is brought forward and planted on the ground to support it. Thus the muscles of the left calf are assisted in their action by those muscles on the front of the trunk and legs which, by their contraction, pull the body forwards; and of course, if the trunk form a slanting line, with the inclination forwards, it is plain that when the heel is raised by the calf-muscles, the whole body will be raised, and pushed obliquely forwards and upwards. The successive acts in taking the first step in walking are represented in fig. 166, 1, 2, 3.

Now it is evident that by the time the body has assumed the position No. 3, it is time that the right leg should be brought forward to support it and prevent it from falling prostrate. This advance of the other leg (in this case the *right*) is effected partly by its mechanically swinging forwards, pendulum-wise, and partly by muscular action; the muscles used being,—1*st*, those on the front of the *thigh*, which bend the thigh forwards on the pelvis, especially the rectus femoris, with the psoas and the iliacus; 2*ndly*, the hamstring muscles, which slightly bend the *leg* on the thigh; and 3*rdly*, the muscles on the front of the *leg*, which raise the front of the foot and toes, and so prevent the latter in swinging forwards from hitching in the ground. Anybody who has attentively watched the helpless flapping action of the foot and leg in cases of partial paralysis affecting the muscles of the leg, or who will, in his own case, note the act of bringing the leg forward in walking, will be convinced of the large share which the muscles take in the act in question; although, of course, their work is rendered much easier by the pendulum-like swinging forward of the leg by its own weight.

The second part of the act of walking, which has been just described, is shown in the diagram (4, fig. 166).

When the *right* foot has reached the ground the action of the *left* leg has not ceased. The calf-muscles of the latter continue to act, and by pulling up the heel, throw the body still more forwards over the *right* leg, now bearing nearly the whole weight, until it is time that in *its* turn the *left* leg should swing forwards, and the left foot be planted on the ground to prevent the body from falling prostrate. As at first, while the calf-muscles of one leg and foot are preparing, so to speak, to *push* the body forward and upward from behind by raising the heel, the muscles on the *front* of the trunk and of the same leg (and of the other leg, except when it is swinging forwards) are helping the act by *pulling* the legs and trunk, so as to make

them incline forward, the rotation in the inclining forwards being effected mainly at the ankle-joint. Two main kinds of leverage are, therefore, employed in the act of walking, and if this idea be firmly grasped, the detail will be understood with comparative ease. One kind of leverage employed in walking is essentially the same with that employed in pulling forward the pole, as in fig. 165. And the other, less exactly, is that employed in raising the handles of a wheelbarrow. Now, supposing the lower end of the pole to be placed in the barrow, we should have a very rough and inelegant, but not altogether bad representation of the two main levers employed in the act of walking. The body is *pulled* forward by the muscles in front, much in the same way, that the pole might be by the force applied at P, (fig. 165) while the raising of the heel and *pushing* forwards of the trunk by the calf-muscles is roughly represented on raising the handles of the barrow. The manner in which these actions are performed alternately by each leg, so that one after the other is swung forwards to support the trunk, which is at the same time *pushed* and *pulled* forwards by the muscles of the other, may be gathered from the previous description.

There is one more thing to be noticed especially in the act of walking. Inasmuch as the body is being constantly supported and balanced on each leg alternately, and therefore on only one at the same moment, it is evident that there must be some provision made for throwing the centre of gravity over the line of support formed by the bones of each leg, as, in its turn, it supports the weight of the body. This may be done in various ways, and the manner in which it is effected is one element in the differences which exist in the walking of different people. Thus it may be done by an instinctive slight rotation of the pelvis on the head of each femur in turn, in such a manner that the centre of gravity of the body shall fall over the foot of this side. Thus when the body is pushed

onwards and upwards by the raising, say, of the *right* heel, as in fig. 166, 3, the pelvis is instinctively, by various muscles, made to rotate on the head of the left femur at the acetabulum, to the left side, so that the weight may fall over the line of support formed by the left leg at the time that the *right* leg is swinging forwards, and leaving all the work of support to fall on its fellow. Such a 'rocking' movement of the trunk and pelvis, however, is but an awkward manner of doing what can be done more gracefully by combining a slight 'rocking' with a movement of the whole trunk and leg over the foot which is being planted on the ground (fig. 167); the action being accompanied with a compensatory outward movement at the hip, more easily appreciated by looking at the figure (167) than described.

Fig. 167.

Thus the body in walking is continually rising and swaying alternately from one side to the other, as its centre of gravity has to be brought alternately over one or other leg; and the curvatures of the spine are altered in correspondence with the varying position of the weight which it has to support. The extent to which the body is raised or swayed differs much in different people.

In walking, one foot or the other is always on the ground. The act of *leaping*, or *jumping*, consists in so sudden a raising of the heels by the sharp and strong contraction of

the calf-muscles, that the body is jerked off the ground. At the same time the effect is much increased by first bending the thighs on the pelvis, and the legs on the thighs, and then suddenly straightening out the angles thus formed. The share which this action has in producing the effect may be easily known by attempting to leap in the upright posture, with the legs quite straight.

Running is performed by a series of rapid low jumps with each leg alternately; so that, during each complete muscular act concerned, there is a moment when both feet are off the ground.

In all these cases, however, the description of the manner in which any given effect is produced, can give but a very imperfect idea of the infinite number of combined and harmoniously arranged muscular contractions which are necessary for even the simplest acts of locomotion.

Actions of the Involuntary Muscles.—The involuntary muscles are for the most part not attached to bones arranged to act as levers, but enter into the formation of such hollow parts as require a diminution of their calibre by muscular action, under particular circumstances. Examples of this action are to be found in the intestines, urinary bladder, heart and blood-vessels, gall-bladder, gland-ducts, etc.

The difference in the manner of contraction of the striated and non-striated fibres has been already referred to (p. 590); and the peculiar vermicular or peristaltic action of the latter fibres in some regions of the body has been described at p. 345.

Source of Muscular Action.

It was formerly supposed that each act of contraction on the part of a muscle was accompanied by a correlative waste or destruction of its own substance; and that the quantity of the nitrogenous excreta, especially of urea, presumably the expression of this waste, was in exact pro-

portion to the amount of muscular work performed. It has been found, however, both that the theory itself is erroneous, and that the supposed facts on which it was founded do not exist.

It is true that in the action of muscles, as of all other parts, there is a certain destruction of tissue or, in other words, a certain 'wear and tear,' which may be represented by a slight increase in the quantity of urea excreted: but it is not the *correlative* expression or *only* source of the power manifested. The increase in the amount of urea which is excreted after muscular exertion is by no means so great as was formerly supposed; indeed, it is very slight. And as there is no reason to believe that the waste of muscle-substance can be expressed, with unimportant exceptions, in any other way than by an increased excretion of urea, it is evident that we must look elsewhere than in destruction of muscle, for the source of muscular action. For, it need scarcely be said, all force manifested in the living body must be the correlative expression of force previously latent in the food eaten or the tissue formed; and evidences of force expended in the body must be found in the *excreta*. If, therefore, the *nitrogenous* excreta, represented chiefly by urea, are not in sufficient quantity to account for the work done, we must look to the *non-nitrogenous* excreta as carbonic acid and water, which, presumably, cannot be the expression of wasted muscle-substance.

The quantity of these non-nitrogenous excreta is undoubtedly increased by active muscular efforts, and to a considerable extent; and whatever may be the source of the water, the carbonic acid, at least, is the result of chemical action in the system, and especially of the combustion of non-nitrogenous food, although, doubtless, of nitrogenous food also. We are, therefore, driven to the conclusion,—that the substance of muscles is not wasted in proportion to the work they perform; and

that the non-nitrogenous as well as the nitrogenous foods may, in their combustion, afford the requisite conditions for muscular action. The urgent necessity for *nitrogenous* food, especially after exercise, is probably due more to the need of *nutrition* by the exhausted muscles and other tissues for which, of course, nitrogen is essential, than to such food being superior to *non-nitrogenous* substances as a source of muscular power.

CHAPTER XVIII.

OF VOICE AND SPEECH.

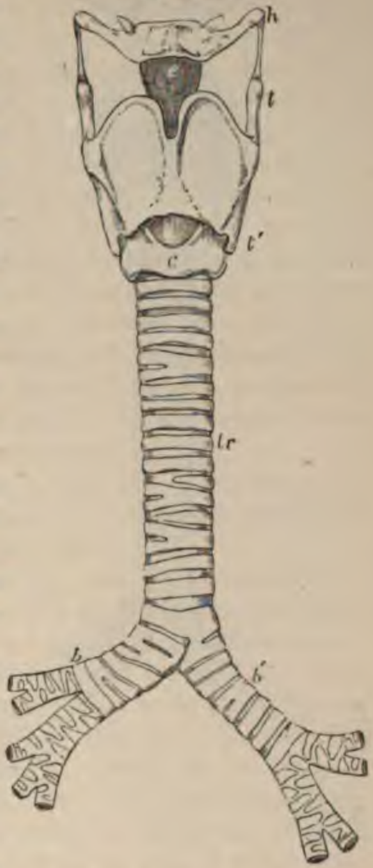
In nearly all air-breathing vertebrate animals there are arrangements for the production of sound, or *voice*, in some part of the respiratory apparatus. In many animals the sound admits of being variously modified and altered during and after its production; and, in man, one of the results of such modification is *speech*.

Mode of Production of the Human Voice.

It has been proved by observations on living subjects, by means of the laryngoscope, as well as by experiments on the larynx taken from the dead body, that the sound of the human voice is the result of the inferior laryngeal ligaments, or true vocal cords (A, *cv*, fig. 172) which bound the glottis, being thrown into vibration by currents of expired air impelled over their edges. Thus, if a free opening exists in the trachea, the sound of the voice ceases, but returns on the opening being closed. An opening into the air-passages above the glottis, on the contrary, does not prevent the voice being formed. Injury of the laryngeal nerves supplying the muscles which move the vocal cords

puts an end to the formation of vocal sounds; and when these nerves are divided on both sides, the loss of voice is complete. Moreover, by forcing a current of air through the larynx in the dead subject, clear vocal sounds are produced, though the epiglottis, the upper ligaments of the larynx or false vocal cords, the ventricles between them, and the inferior ligaments or true vocal cords, and the upper part of the arytenoid cartilages, be all removed; provided the true vocal cords remain entire, with their points of attachment, and be kept tense and so approximated that the fissure of the glottis may be narrow.

Fig. 168.*



The vocal ligaments or cord, therefore, may be regarded as the proper organs of the mere voice: the modifications of the voice are effected by other

* Fig. 168. Outline showing the general form of the larynx, trachea, and bronchi, as seen from before. ½.—*h*, the great cornu of the hyoid bone; *e*, epiglottis; *t*, superior, and *t'*, inferior cornu of the thyroid cartilage; *c*, middle of the cricoid cartilage; *tr*, the trachea, showing sixteen cartilaginous rings; *b*, the right, and *b'*, the left bronchus.

Fig. 169.*

parts as well as by them. Their structure is adapted to enable them to vibrate like tense membranes, for they are essentially composed of elastic tissue; and they are so attached to the cartilaginous parts of the larynx that their position and tension can be variously altered by the contraction of the muscles which act on these parts.

The Larynx.

The *larynx*, or organ of voice, consists essentially of two elastic lips called the vocal cords, which are so attached to certain cartilages, and so under the control of certain muscles, that they

* Fig. 169. Outline showing the general form of the larynx, trachea, and bronchi as seen from behind. $\frac{1}{2}$.—*h*, great cornu of the hyoid bone; *t*, superior, and *t'*, the inferior cornu of the thyroid cartilage: *e*, the epiglottis; *a*, points to the back of both the arytenoid cartilages, which are surmounted by the cornicula; *c*, the middle ridge on the back of the cricoid cartilage; *t r*, the posterior membranous part of the trachea; *b*, *b'*, right and left bronchi.

can be made the means not only of closing the larynx against the entrance and exit of air to or from the lungs, but also can be stretched or relaxed, shortened or lengthened, in accordance with the conditions that may be necessary for the air in passing over them, to set them vibrating and produce various sounds. Their action in respiration has been already referred to (p. 200), in connection with ordinary tranquil respiration, and also (p. 222, *et seq.*) with other respiratory acts, in which the opening or closing of the glottis, or, in other words, the close apposition or separation of the vocal cords, is an essential part of the performance. In these respiratory acts, however, any sound that may be produced, as in coughing, is, so to speak, an accident, and not performed with purpose. In the present chapter the sound produced by the vibration of the vocal cords is the only part of their function with which we have to deal.

It will be well, perhaps, to refer to a few points in the anatomy of the larynx, before considering its physiology in connection with voice and speech.

The principal parts entering into the formation of the larynx (figs. 169 and 170) are—(*t*) the thyroid cartilage; (*c*) the cricoid cartilage; (*a*) the two arytenoid cartilages; and the two true vocal cords (A, *cv*, fig. 172). The epiglottis, (fig. 170, *e*) has but little to do with the voice, and is chiefly useful in falling down as a 'lid' over the upper part of the larynx, to prevent the entrance of food and drink in deglutition. The false vocal cords (*cvs*, fig. 172), and the ventricle of the larynx, which is a space between the false and the true cord of either side, need be here only referred to.

The thyroid cartilage (fig. 170, 1 to 4) does not form a complete ring around the larynx, but only covers the front portion. The cricoid cartilage (fig. 170, 5, 6), on the other hand, is a complete ring; the back part of the ring being much broader than the front. On the top of this broad por-

tion of the cricoid are the arytenoid cartilages (fig. 169, *a*) the connection between the cricoid below and arytenoid cartilages above being a joint with synovial membrane and ligaments, the latter permitting tolerably free motion between them. But, although the arytenoid cartilages can move on the cricoid, they of course accompany the latter in all their movements, just as the head may nod or turn on the top of the spinal column, but must accompany it in all its movements as a whole.

Fig. 170*.

The thyroid cartilage is also connected with the cricoid, not only by ligaments, but by two joints with synovial membrane (t′, figs. 168 and 169); the lower *cornua* of the thyroid clasping, or nipping, as it were, the cricoid between them, but not so tightly but that the thyroid can revolve, within a certain range, around an axis passing transversely through the two joints at which the cricoid is clasped. The vocal cords are attached (behind) to the front portion of the base of the arytenoid cartilages, and (in front) to the re-entering angle at the back part of the thyroid; it is evident, therefore, that all movements of either of these cartilages must produce an effect on them of some kind or other. Inasmuch, too, as the arytenoid cartilages rest on the top of the back portion of the cricoid cartilage (*a*, fig. 169), and are connected with it by capsular and other ligaments, all movements of the cricoid cartilage must move the

* Fig. 170. Cartilages of the larynx seen from before. ¾.—1 to 4, thyroid cartilage; 1, vertical ridge or pomum Adami; 2, right ala; 3, superior, and 4, inferior cornu of the right side; 5, 6, cricoid cartilage; 5, inside of the posterior part; 6, anterior narrow part of the ring; 7, arytenoid cartilages.

arytenoid cartilages, and also produce an effect on the vocal cords.

The so-called *intrinsic* muscles of the larynx, or those which, in their action, have a direct action on the vocal cords, are nine in number—four pairs, and a single muscle; namely, two *crico-thyroid* muscles, two *thyro-arytenoid*, two *posterior crico-arytenoid*, two *lateral crico-arytenoid*, and one *arytenoid* muscle. Their actions are as follows:—When the *crico-thyroid* muscles (10, fig. 171) contract, they rotate the cricoid on the thyroid cartilage in such a manner that the upper and back part of the former, and of necessity the arytenoid cartilages on the top of it, are tipped backwards, while the thyroid is inclined forward: and thus, of course, the vocal cords being attached in front to one, and behind to the other, are 'put on the stretch.'

Fig. 171.*

The *thyro-arytenoid* muscles (7, fig. 174), on the other hand, have an opposite action,—pulling the *thyroid* backwards, and the *arytenoid* and upper and back part of the *cricoid* cartilages forwards, and thus *relaxing* the vocal cords.

The *crico-arytenoidei postici* muscles (fig. 173, *b*) *dilate* the glottis, and separate the vocal cords, the one from the other, by an action on the arytenoid cartilage, which will be plain on reference to B′ and C′, (fig. 172). By their

* Fig. 171. Lateral view of exterior of the larynx, after Mr. Willis. 8, thyroid cartilage; 9, Cricoid cartilage; 10, Crico-thyroid muscle; 11, Crico-thyroid ligament; 12, first rings of trachea.

contraction they tend to *pull together* the outer angles of the arytenoid cartilages in such a fashion as to rotate the latter at their joint with the cricoid, and of course to throw asunder their anterior angles to which the vocal cords are attached.

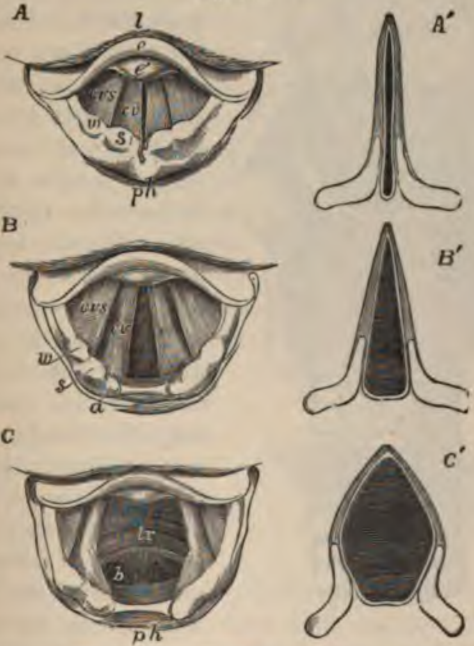
These *posterior* crico-arytenoid muscles are opposed by the *crico-arytenoidei laterales*, which, pulling in the opposite direction from the other side of the axis of rotation, have of course exactly the opposite effect, and close the glottis (fig. 174, 4 and 5).

The aperture of the glottis can be also contracted by the *arytenoid* muscle (*s*, fig. 173, and 6, fig. 174), which, in its contraction, pulls together the upper parts of the arytenoid cartilages between which it extends.

The placing of the vocal cords in a position parallel one with the other, is effected by a combined action of the various little muscles which act on them—the thyro-arytenoidei having, without much reason, the credit of taking the largest share in the production of this effect. Fig. 172 is intended to show the various positions of the vocal cords under different circumstances. Thus, in ordinary tranquil breathing, the opening of the glottis is wide and triangular, becoming a little wider at each inspiration, and a little narrower at each expiration (fig. 172, see also p. 200). On making a rapid and deep inspiration the opening of the glottis is widely dilated, as in C, fig. 172, and somewhat lozenge-shaped. At the moment of the emission of sound, it is more narrowed, the margins of the arytenoid cartilages being brought into contact, and the edges of the vocal cords approximated and made parallel, at the same time that their tension is much increased. The higher the note produced, the tenser do the cords become (fig. 172, A); and the range of a voice depends, of course, in the main, on the extent to which the degree of tension of the vocal cords can be thus altered. In the production of a high note, the vocal cords are brought well within sight, so as to be

plainly visible with the help of the laryngoscope. In the utterance of grave tones, on the other hand, the epiglottis is depressed and brought over them, and the arytenoid

Fig. 172.*



* Fig. 172. Three laryngoscopic views of the superior aperture of the larynx and surrounding parts and different states of the glottis during life (from Czermak).

A, the glottis during the emission of a high note in singing; B, in easy and quiet inhalation of air; C, in the state of widest possible dilatation, as in inhaling a very deep breath. The diagrams A′, B′, and C′, have been added to Czermak's figures, to show in horizontal sections of the glottis the position of the vocal ligaments and arytenoid cartilages in the three several states represented in the other figures. In all the figures, so far as marked, the letters indicate the parts as follows, viz.: *l*, the base of the tongue; *e*, the upper free part of the epiglottis; *e*, the tubercle or cushion of the epiglottis; *ph*, part of the anterior wall of the pharynx behind the larynx; in the margin of the aryteno-epiglottidean fold *w*, the swelling of the membrane caused by the cartilages of

cartilages look as if they were trying to hide themselves under it (fig. 175).

The *epiglottis*, by being somewhat pressed down so as to cover the superior cavity of the larynx, serves to render the notes deeper in tone, and at the same time somewhat duller, just as covering the end of a short tube placed in front of caoutchouc tongues lowers the tone. In no other respect does the epiglottis appear to have any effect in modifying the vocal sounds.

Fig. 173.*

The degree of approximation of the vocal cords also usually corresponds with the height of the note produced; but probably not always, for the width of the aperture has no essential influence on the height of the note, as long as the vocal cords

Wrisberg; *s*, that of the cartilages of Santorini; *a*, the tip or summit of the arytenoid cartilages; *c v*, the true vocal cords or lips of the rima glottidis; *c v s*, the superior or false vocal cords; between them the ventricle of the larynx; in C, *tr* is placed on the anterior wall of the receding trachea, and *b* indicates the commencement of the two bronchi beyond the bifurcation which may be brought into view in this state of extreme dilatation (from Quain's Anatomy).

* Fig. 173. View of the larynx and part of the trachea from behind, with the muscles dissected; *h*, the body of the hyoid bone; *e*, epiglottis; *t*, the posterior borders of the thyroid cartilage; *c*, the median ridge of the cricoid; *a*, upper part of the arytenoid; *s*, placed on one of the oblique fasciculi of the arytenoid muscle; *b*, left posterior crico-arytenoid muscle; ends of the incomplete cartilaginous rings of the trachea; *l*, fibrous membrane crossing the back of the trachea; *n*, muscular fibres exposed in a part (from Quain's Anatomy).

have the same tension; only with a wide aperture, the tone is more difficult to produce, and is less perfect, the rushing of the air through the aperture being heard at the same time.

Fig. 147.*

No true vocal sound is produced at the posterior part of the aperture of the glottis, that, viz., which is formed by the space between the arytenoid cartilages. For, as Müller's experiments showed, if the arytenoid cartilages be approximated in such a manner that their anterior processes touch each other, but yet leave an opening behind them as well as in front, no second vocal tone is produced by the passage of the air through the posterior opening, but merely a rustling or bubbling sound; and the height or pitch of the note produced is the same whether the posterior part of the glottis be open or not, provided the vocal cords maintain the same degree of tension.

Fig. 175.†

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* Fig. 174. View of the interior of larynx from above. 1, aperture of glottis; 2, arytenoid cartilages; 3, vocal cords; 4, posterior crico-arytenoid muscles; 5, lateral crico-arytenoid muscle of right side, that of left side removed; 6, arytenoid muscle; 7, thyro-arytenoid muscle of left side, that of right side removed; 8, thyroid cartilage; 9, cricoid cartilage; 13, posterior crico-arytenoid ligament. With the exception of the arytenoid muscle, this diagram is a copy from Mr. Willis's figure.

†. Fig. 175. View of the upper part of the larynx as seen by means of the laryngoscope during the utterance of a grave note. *c*, epiglottis; *s*, tubercles of the cartilages of Santorini; *a*, arytenoid cartilages; *z*, base of the tongue; *ph*, the posterior wall of the pharynx.

Application of the Voice in Singing and Speaking.

The notes of the voice thus produced may observe three different kinds of sequence. The first is the monotonous, in which the notes have nearly all the same pitch as in ordinary speaking; the variety of the sounds of speech being due to articulation in the mouth. In speaking, however, occasional syllables generally receive a higher intonation for the sake of accent. The second mode of sequence is the successive transition from high to low notes, and *vice versâ*, without intervals; such as is heard in the sounds, which, as expressions of passion, accompany crying in men, and in the howling and whining of dogs. The third mode of sequence of the vocal sounds is the musical, in which each sound has a determinate number of vibrations, and the numbers of the vibrations in the successive sounds have the same relative proportions that characterise the notes of the musical scale.

The *compass of the voice* in different individuals, comprehends one, two, or three octaves. In singers—that is, in persons apt for singing—it extends to two or three octaves. But the male and female voices commence and end at different points of the musical scale. The lowest note of the female voice is about an octave higher than the lowest of the male voice; the highest note of the female voice about an octave higher than the highest of the male. The compass of the male and female voices taken together, or the entire scale of the human voice, includes about four octaves. The principal difference between the male and female voice is, therefore, in their pitch; but they are also distinguished by their tone,—the male voice is not so soft.

The voice presents other varieties besides that of male and female; there are two kinds of male voice, technically called the bass and tenor, and two kinds of female voice, the contralto and soprano, all differing from each other in

tone. The bass voice usually reaches lower than the tenor and its strength lies in the low notes; while the tenor voice extends higher than the bass. The contralto voice has generally lower notes than the soprano, and is strongest in the lower notes of the female voice; while the soprano voice reaches higher in the scale. But the difference of compass, and of power in different parts of the scale, is not the essential distinction between the different voices; for bass singers can sometimes go very high, and the contralto frequently sings the high notes like soprano singers. The essential difference between the bass and tenor voices, and between the contralto and soprano, consists in their tone or 'timbre,' which distinguishes them even when they are singing the same note. The qualities of the barytone and mezzo-soprano voices are less marked; the barytone being intermediate between the bass and tenor, the mezzo-soprano between the contralto and soprano. They have also a middle position as to pitch in the scale of the male and female voices.

The different pitch of the male and the female voice depends on the different length of the vocal cords in the two sexes; their relative length in men and women being as three to two. The difference of the two voices in tone or 'timbre,' is owing to the different nature and form of the resounding walls, which in the male larynx are much more extensive, and form a more acute angle anteriorly. The different qualities of the tenor and bass, and of the alto and soprano voices, probably depend on some peculiarities of the ligaments, and the membranous and cartilaginous parietes of the laryngeal cavity, which are not at present understood, but of which we may form some idea, by recollecting that musical instruments made of different materials, *e.g.*, metallic and gut-strings, may be tuned to the same note, but that each will give it with a peculiar tone or 'timbre.'

The larynx of boys resembles the female larynx; their

vocal cords before puberty have not two-thirds the length which they acquire at that period; and the angle of their thyroid cartilage is as little prominent as in the female larynx. Boys' voices are alto and soprano, resembling in pitch those of women, but louder, and differing somewhat from them in tone. But, after the larynx has undergone the change produced during the period of development at puberty, the boy's voice becomes bass or tenor. While the change of form is taking place, the voice is said to 'crack;' it becomes imperfect, frequently hoarse and crowing, and is unfitted for singing until the new tones are brought under command by practice. In eunuchs, who have been deprived of the testes before puberty, the voice does not undergo this change. The voice of most old people is deficient in tone, unsteady, and more restricted in extent: the first defect is owing to the ossification of the cartilages of the larynx and the altered condition of the vocal cord; the want of steadiness arises from the loss of nervous power and command over the muscles; the result of which is here, as in other parts, a tremulous motion. These two causes combined render the voices of old people void of tone, unsteady, bleating, and weak.

In any class of persons arranged, as in an orchestra, according to the characters of voices, each would possess, with the general characteristics of a bass, or tenor, or any other kind of voice, some peculiar character by which his voice would be recognized from all the rest. The conditions that determine these distinctions are, however, quite unknown. They are probably inherent in the tissues of the larynx, and are as indiscernible as the minute differences that characterize men's features; one often observes, in like manner, hereditary and family peculiarities of voice as well marked as those of the limbs or face.

Most persons, particularly men, have the power, if at all

capable of singing, of modulating their voices through a double series of notes of different character: namely, the notes of the natural voice, or *chest-notes*, and the *falsetto notes*. The natural voice, which alone has been hitherto considered, is fuller, and excites a distinct sensation of much stronger vibration and resonance than the falsetto voice, which has more a flute-like character. The deeper notes of the male voice can be produced only with the natural voice, the highest with the falsetto only; the notes of middle pitch can be produced either with the natural or falsetto voice; the two registers of the voice are therefore not limited in such a manner as that one ends when the other begins, but they run in part side by side.

The natural, or chest-notes, are produced by the ordinary vibrations of the vocal cords. The mode of production of the falsetto notes is still obscure. By Müller they are thought to be due to vibrations of only the inner borders of the vocal cords. In the opinion of Petrequin and Diday, they do not result from vibrations of the vocal cords at all, but from vibrations of the air passing through the aperture of the glottis, which they believe assumes, at such times, the contour of the *embouchure* of a flute. Others (considering some degree of similarity which exists between the falsetto notes, and the peculiar tones called harmonic, which are produced when, by touching or stopping a harp-string at a particular point, only a portion of its length is allowed to vibrate) have supposed that, in the falsetto notes, portions of the vocal ligaments are thus isolated, and made to vibrate while the rest are held still. The question cannot yet be settled; but any one in the habit of singing may assure himself, both by the difficulty of passing smoothly from one set of notes to the other, and by the necessity of exercising himself in both registers, lest he should become very deficient in one, that there must be some great difference in the modes in which their respective notes are produced.

The strength of the voice depends partly on the degree to which the vocal cords can be made to vibrate; and partly on the fitness for resonance of the membranes and cartilages of the larynx, of the parietes of the thorax, lungs, and cavities of the mouth, nostrils, and communicating sinuses. It is diminished by anything which interferes with such capability of vibration. The intensity or loudness of a given note with maintenance of the same 'pitch,' cannot be rendered greater by merely increasing the force of the current of air through the glottis; for increase of the force of the current of air, *cæteris paribus*, raises the pitch both of the natural and the falsetto notes. Yet, since a singer possesses the power of increasing the loudness of a note from the faintest 'piano' to 'fortissimo' without its pitch being altered, there must be some means of compensating the tendency of the vocal cords to emit a higher note when the force of the current of air is increased. This means evidently consists in modifying the tension of the vocal cords. When a note is rendered louder and more intense, the vocal cords must be relaxed by remission of the muscular action, in proportion as the force of the current of the breath through the glottis is increased. When a note is rendered fainter, the reverse of this must occur.

The *arches of the palate and the uvula* become contracted during the formation of the higher notes; but their contraction is the same for a note of given height, whether it be falsetto or not; and in either case the arches of the palate may be touched with the finger, without the note being altered. Their action, therefore, in the production of the higher notes seems to be merely the result of involuntary associate nervous action, excited by the voluntarily increased exertion of the muscles of the larynx. If the palatine arches contribute at all to the production of the higher notes of the natural voice and the falsetto, it can only be by their increased tension strengthening the resonance.

The office of the *ventricles of the larynx* is evidently to afford a free space for the vibrations of the lips of the glottis; they may be compared with the cavity at the commencement of the mouth-piece of trumpets, which allows the free vibration of the lips.

SPEECH.

Besides the musical tones formed in the larynx, a great number of other sounds can be produced in the vocal tubes, between the glottis and the external apertures of the air-passages, the combination of which sounds into different groups to designate objects, properties, actions, etc., constitutes *language*. The languages do not employ all the sounds which can be produced in this manner, the combination of some with others being often difficult. Those sounds which are easy of combination enter, for the most part, into the formation of the greater number of languages. Each language contains a certain number of such sounds, but in no one are all brought together. On the contrary, different languages are characterised by the prevalence in them of certain classes of these sounds, while others are less frequent or altogether absent.

The sounds produced in speech, or *articulate sounds*, are commonly divided into *vowels* and *consonants;* the distinction between which is, that the sounds for the former are generated by the larynx, while those for the latter are produced by interruption of the current of air in some part of the air-passages above the larynx. The term consonant has been given to these because several of them are not properly sounded, except *consonantly with* a vowel. Thus, if it be attempted to pronounce aloud the consonants *b*, *d*, and *g*, or their modifications, *p*, *t*, *k*, the intonation only follows them in their combination with a vowel.

To recognize the essential properties of the articulate sounds, we must, according to Müller first examine them as they are produced in whispering, and then investigate

which of them can also be uttered in a modified character conjoined with local tone. By this procedure we find two series of sounds: in one the sounds are mute, and cannot be uttered with a vocal tone; the sounds of the other series can be formed independently of voice, but are also capable of being uttered in conjunction with it.

All the vowels can be expressed in a whisper without vocal tone, that is, mutely. These mute vowel-sounds differ, however, in some measure, as to their mode of production, from the consonants. All the mute consonants are formed in the vocal-tube above the glottis, or in the cavity of the mouth or nose, by the mere rushing of the air between the surfaces differently modified in disposition. But the sound of the vowels, even when mute, has its source in the glottis, though its vocal cords are not thrown into the vibrations necessary for the production of voice; and the sound seems to be produced by the passage of the current of air between the relaxed vocal cords. The same vowel sound can be produced in the larynx when the mouth is closed, the nostrils being open, and the utterance of all vocal tone avoided. This sound, when the mouth is open, is so modified by varied forms of the oral cavity, as to assume the characters of the vowels *a, i, o, u*, in all their modifications.

The cavity of the mouth assumes the same form for the articulation of each of the mute vowels as for the corresponding vowel when vocalized; the only difference in the two cases lies in the kind of sound emitted by the larynx. Krantzenstein and Kempelen have pointed out that the conditions necessary for changing one and the same sound into the different vowels, are differences in the size of two parts—the oral canal and the oral opening; and the same is the case with regard to the mute vowels. By oral canal, Kempelen means here the space between the tongue and palate: for the pronunciation of certain vowels both the opening of the mouth and the space just

mentioned are widened; for the pronunciation of other vowels both are contracted; and for others one is wide, the other contracted. Admitting five degrees of size, both of the opening of the mouth and of the space between the tongue and palate, Kempelen thus states the dimensions of these parts for the following vowel sounds :—

Vowel.	Sound.	Size of oral opening.	Size of oral canal.
a as in	'far'	5	3
a ,,	'name'	4	2
e ,,	'theme'	3	1
o ,,	'go'	2	4
oo ,,	'cool'	1	5

Another important distinction in articulate sounds is, that the utterance of some is only of momentary duration, taking place during a sudden change in the conformation of the mouth, and being incapable of prolongation by a continued expiration. To this class belong *b*, *p*, *d*, and the hard *g*. In the utterance of other consonants the sounds may be *continuous;* they may be prolonged, *ad libitum*, as long as a particular disposition of the mouth and a constant expiration are maintained. Among these consonants are *h*, *m*, *n*, *f*, *s*, *r*, *l*. Corresponding differences in respect to the time that may be occupied in their utterance exist in the vowel-sounds, and principally constitute the differences of long and short syllables. Thus, the *a* as in "far" and "fate," the *o* as in "go" and "fort," may be indefinitely prolonged; but the same vowels (or more properly different vowels expressed by the same letters), as in "can" and "fact," in "dog" and "rotten," cannot be prolonged.

All sounds of the first or explosive kind are insusceptible of combination with vocal tone ("intonation"), and are absolutely mute; nearly all the consonants of the second or continuous kind may be attended with "intonation."

The peculiarity of speaking, to which the term *ventriloquism* is applied, appears to consist merely in the

varied modification of the sounds produced in the larynx, in imitation of the modifications which voice ordinarily suffers from distance, etc. From the observations of Müller and Colombat, it seems that the essential mechanical parts of the process of ventriloquism consist in taking a full inspiration, then keeping the muscles of the chest and neck fixed, and speaking with the mouth almost closed, and the lips and lower jaw as motionless as possible, while air is very slowly expired through a very narrow glottis; care being taken also, that none of the expired air passes through the nose. But, as observed by Müller, much of the ventriloquist's skill in imitating the voices coming from particular directions, consists in deceiving other senses than hearing. We never distinguish very readily the direction in which sounds reach our ear; and, when our attention is directed to a particular point, our imagination is very apt to refer to that point whatever sounds we may hear.

The tongue, which is usually credited with the power of speech,—*language* and speech being often employed as synonymous terms—plays only a subordinate, although very important part. This is well shown by cases in which nearly the whole organ has been removed on account of disease. Patients who recover from this operation talk imperfectly, and their voice is considerably modified; but the loss of speech is confined to those letters, in the pronunciation of which the tongue is concerned.

CHAPTER XIX.

THE SENSES.

Sensation consists in the mind receiving, through the medium of the nervous system, and, usually as the result of the action of an external cause, a knowledge of certain

qualities or conditions, not of external bodies but of the nerves of sense themselves; and these qualities of the nerves of sense are in all different, the nerve of each sense having its own peculiar quality.

There are two principal kinds of sensation, named common and special. The first is the consequence of the ordinary sensibility or feeling possessed by most parts of the body, and is manifested when a part is touched, or in any ordinary manner is stimulated. According to the stimulus, the mind perceives a sensation of heat, or cold, of pain, of the contact of hard, soft, smooth, or rough objects, etc. From this, also, in morbid states, the mind perceives itching, tingling, burning, aching and the like sensations. In its greatest perfection, common sensibility constitutes *touch* or *tact*. Touch is, indeed, usually classed with the special senses, and will be considered in the same group with them; yet it differs from them in being a property common to many nerves, *e.g.*, all the sensitive spinal nerves, the pneumogastric, glosso-pharyngeal, and fifth cerebral nerves, and in its impressions being communicable through many organs.

Including the sense of touch, the special senses are five in number,—the senses of sight, hearing, smell, taste, and touch. The manifestation of each of the first three depends on the existence of a special nerve; the optic for the sense of sight, the auditory for that of hearing, and the olfactory for that of smell. The sense of taste appears to be a property common to branches of the fifth and of the glosso-pharyngeal nerves.

The senses, by virtue of the peculiar properties of their several nerves, make us acquainted with the states of our own body; and thus indirectly inform us of such qualities and changes of external matter as can give rise to changes in the condition of the nerves. That which through the medium of our senses is actually perceived by the mind is, indeed, merely a property or change of condition of our

nerves; but the mind is accustomed to interpret these modifications in the state of the nerves produced by external influences as properties of the external bodies themselves. This mode of regarding sensations is so habitual in the case of the senses which are more rarely affected by internal causes, that it is only on reflection that we perceive it to be erroneous. In the case of the sense of feeling, on the contrary, where many of the peculiar sensations of the nerves perceived by the sensorium are excited as frequently by internal as by external causes, we more readily apprehend the truth. For it is easily conceived that the feeling of pain or pleasure, for example, is due to a condition of the nerves, and is not a property of the things which excite it. What is true of these is true of all other sensations; the mind perceives conditions of the optic, olfactory, and other nerves specifically different from that of their state of rest; these conditions may be excited by the contact of external objects, but they may also be the consequence of internal changes: in the former case the mind, having knowledge of the object through either instinct or instruction, recognizes it by the appropriate changes which it produces in the state of the nerves.

The special susceptibility of the different nerves of sense for certain influences,—as of the optic nerve, or rather its centre, for light; of the auditory nerve, or centre, for vibrations of the air, etc., and so on,—is not due entirely to those nerves having each a specific irritability for such influences exclusively. For although, in the ordinary events of life, the optic nerve is excited only by the undulations or emanations of which light may consist, the auditory only by vibrations of the air, and the olfactory only by odorous particles—yet each of these nerves may have its peculiar properties called forth by other conditions. In fact, in whatever way and to whatever degree a nerve of special sense is stimulated, the sensation produced is essentially of the same kind; irritation of the optic nerve

invariably producing a sensation of light, of the auditory nerve a sensation of some modification of sound. The phenomenon must, therefore, be ascribed to a peculiar quality belonging to each nerve of special sense. It has been supposed, indeed, that irritation of a nerve of special sense, when excessive, may produce pain; but experiments seem to have proved that none of these nerves possess the faculty of common sensibility. Thus Magendie observed that when the olfactory nerves laid bare in a dog were pricked, no signs of pain were manifested; and other experiments of his seemed to show that both the retina and optic nerve are insusceptible of pain.

External impressions on a nerve can give rise to no kind of sensation which cannot also be produced by internal causes, exciting changes in the condition of the same nerve. In the case of the sense of touch, this is at once evident. The sensations of the nerves of touch (or common sensibility), excited by causes acting from without, are those of cold and heat, pain and pleasure, and innumerable modifications of these, which have the same kind of sensation as their element. All these sensations are constantly being produced by internal causes, in all parts of our body endowed with sensitive nerves. The sensations of the nerves of touch are therefore states or qualities proper to themselves, and merely rendered manifest by exciting causes, whether external or internal. The sensation of smell, also, may be perceived independently of the application of any odorous substance from without, through the influence of some internal condition of the nerve of smell. The sensations of the sense of vision, namely, colour, light, and darkness, are also often perceived independently of all external exciting causes. So, also, whenever the auditory nerve is in a state of excitement, the sensations peculiar to it, as the sounds of ringing, humming, etc., are perceived.

The same cause, whether internal or external, excites in the different senses different sensations; in each sense the

sensations peculiar to it. For instance, one uniform *internal* cause, which may act on all the nerves of the senses in the same manner, is the accumulation of blood in their capillary vessels, as in congestion and inflammation. This one cause excites in the retina, while the eyes are closed, the sensations of light and luminous flashes; in the auditory nerve, the sensation of humming and ringing sounds; in the olfactory nerve, the sense of odours; and in the nerves of feeling, the sensation of pain. In the same way, also, a narcotic substance introduced into the blood, excites in the nerves of each sense peculiar symptoms; in the optic nerves, the appearance of luminous sparks before the eyes; in the auditory nerves, "tinnitus aurium"; and in the common sensitive nerves, the sensation of creeping over the surface. So, also, among *external* causes, the stimulus of electricity, or the mechanical influence of a blow, concussion, or pressure, excites in the eye the sensation of light and colours; in the ear, a sense of a loud sound or of ringing; in the tongue, a saline or acid taste; and at the other parts of the body, a perception of peculiar jarring or of the mechanical impression, or a shock like it.

Although, in the cases just referred to, and in all ordinary conditions, sensations are derived from peculiar conditions of the nerves of sense, whether excited by external or by internal causes, yet the mind may have the same sensations independently of changes in the conditions of at least the peripheral portions of the several nerves, and even independently of any connection with the external organs of the senses. The causes of such sensations are seated in the parts of the brain in which the several nerves of sense terminate. Thus pressure on the brain has been observed to cause the sensation of light: luminous spectra may be excited by internal causes after complete amaurosis of the retina: and Humboldt states, that, in a man who had lost one eye, he produced by means of galvanism, luminous appearances on the blind side. Many of the

various morbid sensations attending diseases of the brain, the vision of spectra, and the like, are of the same kind.

Again, although the immediate objects of the perception of our senses are merely particular states induced in the nerves, and felt as sensations, yet, inasmuch as the nerves of the senses are material bodies, and therefore participate in the properties of matter generally, occupying space, being susceptible of vibratory motion, and capable of being variously changed chemically, as well as by the action of heat and electricity, they make known to the mind, by virtue of the different changes thus produced in them by external causes, not merely their own condition, but also some of the different properties and changes of condition of external bodies; as, *e.g.*, progressive and tremulous motion, chemical change, etc. The information concerning external nature thus obtained by the senses, varies in each sense, having a relation to the peculiar qualities or energies of the nerve.

The *sensation of motion* is, like motion itself, of two kinds, —progressive and vibratory. The faculty of the perception of progressive motion is possessed chiefly by the senses of vision, touch, and taste. Thus an impression is perceived travelling from one part of the retina to another, and the movement of the image is interpreted by the mind as the motion of the object. The same is the case in the sense of touch; so also the movement of a sensation of taste over the surface of the organ of taste, can be recognized. The motion of tremors, or vibrations, is perceived by several senses, but especially by those of hearing and touch. For the sense of hearing, vibrations constitute the ordinary stimulus, and so give rise to the perception of sound. By the sense of touch, vibrations are perceived as tremors, occasionally attended with the general impression of tickling; for instance, when a vibrating body, such as a tuning fork, is approximated to a very sensible part of the surface, the eye can communi-

cate to the mind the image of a vibrating body, and can distinguish the vibrations when they are very slow; it may be also that the vibrations are communicated to the optic as to the auditory nerve in such a manner that it repeats them, or receives their impulses.

We are made acquainted with *chemical actions* principally by taste, smell, and touch, and by each of these senses in the mode proper to it. Volatile bodies disturbing the conditions of the nerves by a chemical action, exert the greatest influence upon the organ of smell; and many matters act on that sense which produce no impression upon the organs of taste and touch,—for example, many odorous substances, as the vapour of metals, such as lead, and the vapour of many minerals. Some volatile substances, however, are perceived not only by the sense of smell, but also by the senses of touch and taste, provided they are of a nature adapted to disturb chemically the condition of those organs, and in case of the organ of taste, to be dissolved by the fluids covering it. Thus, the vapours of horse-radish and mustard, and acrid suffocating gases, act upon the conjunctiva and the mucous membrane of the lungs, exciting through the common sensitive nerves, merely modifications of common feeling; and at the same time they excite the sensations of smell and of taste.

Sensations are referred from their proper seat towards the exterior; but this is owing, not to anything in the nature of the nerves themselves, but to the accompanying idea derived from experience. For in the perception of sensations, there is a combined action both of the mind and of the nerves of sense; and the mind by education or experience, has learned to refer the impressions it receives to objects external to the body. Even when it derives impressions from internal causes, it commonly refers them to external objects. The light perceived in congestion of the retina seems external to the body: the ringing of the ears

in disease is felt as if the sound came from some distance: the mind referring it to the outer world from which it is in the habit of receiving the like impression.

Moreover, the mind not only perceives the sensations, and interprets them according to ideas previously obtained, but it has a direct influence upon them, imparting to them intensity by its faculty of attention. Without simultaneous attention, all sensations are only obscurely, if at all, perceived. If the mind be torpid in indolence, or if the attention be withdrawn from the nerves of sense in intellectual contemplation, deep speculations, or an intense passion, the sensations of the nerves make no impression upon the mind; they are not perceived,—that is to say, they are not communicated to the conscious "self," or with so little intensity, that the mind is unable to retain the impression, or only recollects it some time after, when it is freed from the preponderating influence of the idea which had occupied it.

This power of attention to the sensations derived from a single organ, may also be exercised in a single portion of a sentient organ, and thus enable one to discern the detail of what would otherwise be a single sensation. For example, by well-directed attention, one can distinguish each of the many tones simultaneously emitted by an orchestra, and can even follow the weaker tones of one instrument apart from the other sounds, of which the impressions being not attended to are less vividly perceived. So, also, if one endeavours to direct attention to the whole field of vision at the same time, nothing is seen distinctly; but when the attention is directed first to this, then to that part, and analyses the detail of the sensation, the part to which the mind is directed is perceived with more distinctness than the rest of the same sensation.

THE SENSE OF SMELL.

The sense of smell ordinarily requires, for its excitement to a state of activity, the action of external matters, which action produces certain changes in the olfactory nerve; and this nerve is susceptible of an infinite variety of states dependent on the nature of the external stimulus.

The first condition essential to the sense of smell is the existence of a special nerve, the changes in whose condition are perceived as sensations of odour; for no other nerve is capable of these sensations, even though acted on by the same causes. The same substance which excites the sensation of smell in the olfactory nerves may cause another peculiar sensation through the nerves of taste, and may produce an irritating and burning sensation on the nerves of touch; but the sensation of odour is yet separate and distinct from these, though it may be simultaneously perceived. The second condition of smell is a peculiar state of the olfactory nerve, or a peculiar change produced in it by the stimulus or odorous substance.

The material causes of odours are, usually, in the case of animals living in the air, either solids suspended in a state of extremely fine division in the atmosphere; or gaseous exhalations often of so subtile a nature that they can be detected by no other re-agent than the sense of smell itself. The matters of odour must, in all cases, be dissolved in the mucus of the mucous membrane before they can be immediately applied to, or affect the olfactory nerves; therefore a further condition necessary for the perception of odours is, that the mucous membrane of the nasal cavity be moist. When the Schneiderian membrane is dry, the sense of smell is impaired or lost; in the first stage of catarrh, when the secretion of mucus within the nostrils is lessened, the faculty of perceiving odour is either lost, or rendered very imperfect.

In animals living in the air, it is also requisite that the

odorous matter should be transmitted in a current through the nostrils. This is effected by an inspiratory movement, the mouth being closed; hence we have voluntary influence over the sense of smell; for by interrupting respiration we prevent the perception of odours, and by repeated quick inspiration, assisted, as in the act of *sniffing*, by the action of the nostrils, we render the impression more intense (see p. 224).

The human organ of smell is essentially formed by the filaments of the olfactory nerves, distributed in minute

Fig. 176.*

arrangement, in the mucous membrane covering the upper third of the septum of the nose, the superior turbinated or spongy bone, the upper part of the middle turbinated bone, and the upper wall of the nasal cavities beneath the cribriform plates of the ethmoid bones (figs. 176 and 177).

This olfactory region is covered by cells of *cylindrical* epi-

* Fig. 176. Nerves of the septum nasi, seen from the right side (from Sappey after Hirschfeld and Leveillé). ⅔.—I, the olfactory bulb; 1, the olfactory nerves passing through the foramina of the cribriform plate, and descending to be distributed on the septum; 2, the internal or septal twig of the nasal branch of the ophthalmic nerve; 3, naso-palatine nerves.

thelium not provided with cilia; and interspersed with these are peculiar fusiform cells with fine processes, called *olfactory* cells. They are supposed to have some connection with the terminal filaments of the olfactory nerve. The lower, or *respiratory* part, as it is called, of the nasal fossæ is lined by *cylindrical ciliated* epithelium, except in the region of the nostrils, where it is *squamous*.

Fig. 177.*

In all the distribution, the branches of the olfactory nerves retain much of the same soft and greyish texture which distinguishes their trunks (as the olfactory lobes of the brain are called) within the cranium. Their individual filaments, also, are peculiar, more resembling those of the sympathetic nerve than the filaments of the other cerebral nerves do, containing no outer white substance, and being finely granular and nucleated. The branches are distributed principally in close plexuses; but the mode of termination of the filaments is not yet satisfactorily determined.

* Fig. 177. Nerves of the outer walls of the nasal fossæ (from Sappey after Hirschfeld and Leveillé). $\frac{2}{3}$.—1, network of the branches of the olfactory nerve, descending upon the region of the superior and middle turbinated bones; 2, external twig of the ethmoidal branch of the nasal nerve; 3, spheno-palatine ganglion; 4, ramification of the anterior palatine nerves; 5, posterior, and 6, middle divisions of the palatine nerves; 7, branch to the region of the inferior turbinated bone; 8, branch to the region of the superior and middle turbinated bones; 9, naso-palatine branch to the septum cut short (after Sharpey).

The sense of smell is derived exclusively through those parts of the nasal cavities in which the olfactory nerves are distributed; the accessory cavities or sinuses communicating with the nostrils seem to have no relation to it. Air impregnated with the vapour of camphor was injected by Deschamps into the frontal sinus through a fistulous opening, and Richerand injected odorous substances into the antrum of Highmore; but in neither case was any odour perceived by the patient. The purposes of these sinuses appear to be, that the bones, necessarily large for the action of the muscles and other parts connected with them, may be as light as possible, and that there may be more room for the resonance of the air in vocalising. The former purpose, which is in other bones obtained by filling their cavities with fat, is here attained, as it is in many bones of birds, by their being filled with air.

All parts of the nasal cavities, whether or not they can be the seats of the sense of smell, are endowed with common sensibility by the nasal branches of the first and second divisions of the fifth nerve. Hence the sensations of cold, heat, itching, tickling, and pain; and the sensation of tension or pressure in the nostrils. That these nerves cannot perform the function of the olfactory nerves is proved by cases in which the sense of smell is lost, while the mucous membrane of the nose remains susceptible of the various modifications of common sensation or touch. But it is often difficult to distinguish the sensation of smell from that of mere feeling, and to ascertain what belongs to each separately. This is the case particularly with the sensations excited in the nose by acrid vapours, as of ammonia, horse-radish, mustard, etc., which resemble much the sensations of the nerves of touch; and the difficulty is the greater, when it is remembered that these acrid vapours have nearly the same action upon the mucous membrane of the eyelids. It was because the common sensibility of the nose to these irritating substances remained after the

destruction of the olfactory nerves, that Magendie was led to believe the fifth nerve might exercise the special sense.

Animals do not all equally perceive the same odours; the odours most plainly perceived by an herbivorous animal and by a carnivorous animal are different. The Carnivora have the power of detecting most accurately by the smell the special peculiarities of animal matters, and of tracking other animals by the scent; but have apparently very little sensibility to the odours of plants and flowers. Herbivorous animals are peculiarly sensitive to the latter, and have a narrower sensibility to animal odours, especially to such as proceed from other individuals than their own species. Man is far inferior to many animals of both classes in respect of the acuteness of smell; but his sphere of susceptibility to various odours is more uniform and extended. The cause of this difference lies probably in the endowments of the cerebral parts of the olfactory apparatus.

Opposed to the sensation of an agreeable odour is that of a disagreeable or disgusting odour, which corresponds to the sensations of pain, dazzling and disharmony of colours, and dissonance in the other senses. The cause of this difference in the effect of different odours is unknown; but this much is certain, that odours are pleasant or offensive in a relative sense only, for many animals pass their existence in the midst of odours which to us are highly disagreeable. A great difference in this respect is, indeed, observed amongst men: many odours, generally thought agreeable, are to some persons intolerable; and different persons describe differently the sensations that they severally derive from the same odorous substances. There seems also to be in some persons an insensibility to certain odours, comparable with that of the eye to certain colours; and among different persons, as great a difference in the acuteness of the sense of smell as among others in the acuteness of sight. We have no exact proof that a

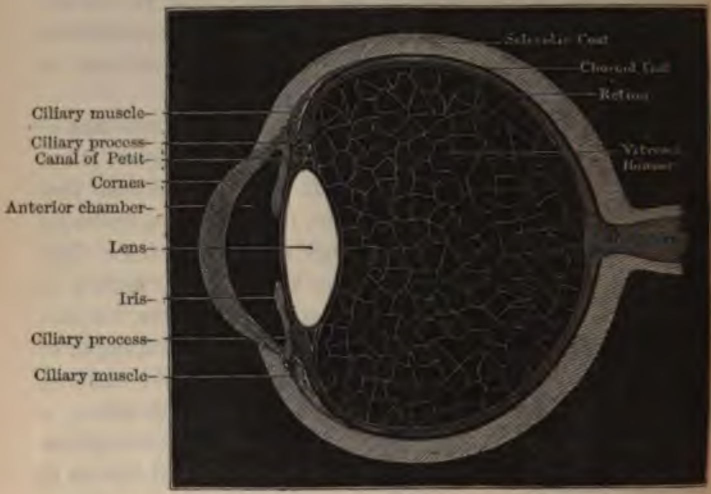
relation of harmony and disharmony exists between odours as between colours and sounds; though it is probable that such is the case, since it certainly is so with regard to the sense of taste; and since such a relation would account in some measure for the different degrees of perceptive power in different persons; for as some have no ear for music (as it is said), so others have no clear appreciation of the relation of odours, and therefore little pleasure in them.

The sensations of the olfactory nerves, independent of the external application of odorous substances, have hitherto been little studied. It has been found that solutions of inodorous substances, such as salts, excite no sensation of odour when injected into the nostrils. The friction of the electric machine is, however, known to produce a smell like that of phosphorus. Ritter, too, has observed, that when galvanism is applied to the organ of smell, besides the impulse to sneeze, and the tickling sensation excited in the filaments of the fifth nerve, a smell like that of ammonia was excited by the negative pole, and an acid odour by the positive pole; whichever of these sensations was produced, it remained constant as long as the circle was closed, and changed to the other at the moment of the circle being opened. Frequently a person smells something which is not present, and which other persons cannot smell; this is very frequent with nervous people, but it occasionally happens to every one. In a man who was constantly conscious of a bad odour, the arachnoid was found after death, by MM. Cullerier and Maignault, to be beset with deposits of bone; and in the middle of the cerebral hemispheres were scrofulous cysts in a state of suppuration. Dubois was acquainted with a man who, ever after a fall from his horse, which occurred several years before his death, believed that he smelt a bad odour.

THE SENSE OF SIGHT.

The eyeball or the organ of vision (fig. 178) consists of a variety of structures which may be thus enumerated:—

Fig. 178.



The *sclerotic*, or outermost coat, envelopes about five-sixths of the eyeball: continuous with it, in front, and occupying the remaining sixth, is the *cornea*. The cornea and front portion of the sclerotic are covered by mucous membrane,—the *conjunctiva*; that which covers the front of the cornea being little more than squamous epithelium. Immediately within the sclerotic is the *choroid* coat, and within the choroid is the *retina*. The interior of the eyeball is well-nigh filled by the *aqueous* and *vitreous humours* and the *crystalline lens*; but also, there is suspended in the interior a contractile and perforated curtain,—the *iris*, for regulating the admission of light, and behind the junction of the sclerotic and cornea is the ciliary muscle, the function of which is to adapt the eye for seeing objects at various distances.

These structures may be now examined rather more in detail.

The *sclerotic* coat is composed of connective tissue, arranged in variously disposed and intercommunicating layers. It is strong, tough, and opaque, and not very elastic.

The *cornea* (fig. 179) is, like the sclerotic, with which it is continuous, chiefly of a fibrous structure, but the fibres are so modified and arranged as to form a transparent membrane for the passage of light. Both in front of and behind the fibrous tissue of the cornea is a structureless elastic membrane with epithelium.

Fig. 179.*

The *choroid*, which is the next tunic of the eye within the sclerotic and immediately outside the retina, consists of a thin and highly vascular membrane, of which the internal surface is covered by a layer of black pigment cells. The principal use of the choroid is to absorb, by means of its pigment, those rays of light which pass through the transparent retina, and thus to prevent their being thrown again upon the retina, so as to interfere

* Fig. 179. Structure of the cornea (after Bowman). A $\frac{60}{1}$, B & C, $\frac{300}{1}$ A, Small portion of a vertical section of the cornea in the adult; *a*, conjunctival epithelium; *b*, anterior elastic lamina; *c* to *d*, fibrous laminæ with nuclear bodies interspersed between them; *c*, fibres shooting through some of these layers from the external elastic lamina; *d*, posterior elastic lamina or membrane of Demours; *e*, internal epithelium of *d*. B, epithelium of the membrane of Demours, as seen looking towards its surface. C, the same seen in section.

Fig. 180.*

Fig. 181.†

with the distinctness of the images there formed. Hence animals in which the choroid is destitute of pigment, and human Albinoes, are dazzled by daylight and see best in the twilight. The choroid coat ends in front in what are called the *ciliary processes* (fig. 180).

The *retina* (fig. 181) is a delicate membrane, concave, with the concavity directed forwards and ending in front, near the outer part of the ciliary processes in a finely notched edge,—the *ora serrata*. Semi-transparent when fresh, it soon becomes clouded and opaque, with a pinkish tint from the blood in its minute

* Fig. 180. Ciliary processes as seen from behind. ⅔.—1, posterior surface of the iris, with the sphincter muscle of the pupil; 2, anterior part of the choroid coat; 3, one of the ciliary processes, of which about seventy are represented.

† Fig. 181. The posterior half of the retina of the left eye viewed from before (after Henle); *s*, the cut edge of the sclerotic coat; *ch*, the choroid; *r*, the retina; in the interior at the middle, the macula lutea with the depression of the fovea centralis is represented by a slight oval shade; towards the left side the light spot indicates the colliculus or eminence at the entrance of the optic nerve, from the centre of which the arteria centralis is seen spreading its branches into the retina, leaving the part occupied by the macula comparatively free.

vessels. It results from the sudden spreading out or expansion of the optic nerve, of whose terminal fibres, apparently deprived of their external white substance, together with nerve-cells, it is essentially composed.

Exactly in the centre of the retina, and at a point thus corresponding to the axis of the eye in which the sense of vision is most perfect, is a round yellowish elevated spot, about $\frac{1}{24}$ of an inch in diameter, having a minute aperture at its summit, and called after its discoverer the *yellow spot of Sœmmering*. It is not covered by the fibrous part of the retina, but a layer of closely-set cells passes over it, and in its centre is a minute depression called *fovea centralis*. About $\frac{1}{10}$ of an inch to the inner side of the yellow spot, and consequently of the axis of the eye, is the point at which the optic nerve spreads out its fibres to form the retina. This is the

Fig. 182.*

* Fig. 182. Vertical section of a small part of the retina (after Kölliker), $\frac{180}{1}$. A, entire section of a small part of the retina; B, two cones represented separately in their connection with the fibres of Müller and other structures; C, two rods represented separately in their connection with the granules, fibres of Müller and the nerve-cells; 1, columnar layer; *a*, in A and C, the rods, in B, the terminal part of the cone; *b*, cones; 2, granular layer; *c*, outer layer of nuclei (striated corpuscles of Henle); *d*, inner layer of nuclei; *f*, inter-nuclear layer; 3, nervous layer; *g*, fine molecular substance outside *h*, the nerve-cells; *k*, nerve-fibres; *l*, membrana limitans; *e*, inner ends of the fibres of Müller resting on the limiting membrane.

only point of the surface of the retina from which the power of vision is absent.

On making a vertical section of the retina, it is seen, under the microscope, to be composed of several layers which differ from each other in structure and arrangement, while besides these there are fibres, the so-called *fibres of Müller*, which extend through the different layers, and perforate them, so to speak. Fig. 182 represents a vertical section of a small piece of the retina. On examination it will be seen that there are three principal layers, bounded on the *inner* aspect by a *membrana limitans*, and on the *outer* by the *choroid* coat. 1. The outermost is the membrane of Jacob, or the *columnar* layer. 2. In the middle is the *granular* layer. 3. The innermost is the *nervous* layer. Each of these layers, again, is composed of different strata, after the fashion shown in the figure.

The columnar layer (Jacob's membrane) is composed of cylindrical or staff-shaped, transparent and highly refractive bodies, arranged perpendicularly to the surface of the retina, with their outer extremities imbedded, to a greater or less depth, in a layer of black pigment of the choroid coat. Recent researches seem to have determined that this membrane, instead of being, as was formerly considered, an independent covering, is intimately associated, both in structure and function, with the sensitive part of the retina; for the conical and staff-shaped bodies, of which it is composed, appear to be connected, by means of delicate fibres issuing from them, with the nerve-vesicles of the retina, and even to become continuous with the radiating processes which some of these vesicles present. Concerning the use of these bodies, the discovery of their connection with the sensitive part of the retina supports the opinion entertained by Kölliker and H. Müller, that their special office is to receive and transmit impressions of light.

The structures of which the *granular layer* is composed are indicated in the figure.

The *nervous* layer is composed of nerve-*corpuscles* and nerve-*fibres*. The nerve-*corpuscles* are the outermost, and are most numerous over the *yellow spot*, and absent altogether from the point of entrance of the optic nerve. They are imbedded in fine molecular matter, which also forms a layer outside them. The nerve-*fibres* radiate as a fine membranous network from the point of entrance of the optic nerve, of whose fibres they are the continuation. They end probably in the nerve-*corpuscles*. The fibres are absent from the yellow spot.

Two of the *fibres of Müller* are, for the sake of illustration, arranged in the figure separately on each side of the layer which they perforate. About the connection of the fibres of Müller there is some uncertainty. They are supposed to be connected by their *outer* ends with the rods and cones; and by their *inner*, which are thought to be modifications of connective tissue, they rest on the *membrana limitans*. Between these points they are supposed to have connections also with some of the other structures through which they pass, especially with the inner layer of nuclei.

The retinal blood-vessels ramify chiefly in the nervous layer.

The structures which have been just described are modified in their distribution over the *yellow spot* in the following manner:—Of the columnar layer, or *membrana Jacobi*, the *cones* greatly predominate; of the nervous layers the *cells* are numerous, while the nerve-*fibres* are absent. There are capillaries here, but none of the larger branches of the retinal arteries. Opposite the *fovea centralis*, there are, moreover, neither the granular, nor the fine molecular layer, nor the fibres of Müller.

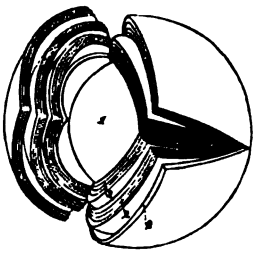
By means of the retina and the other parts just described, a provision is afforded for enabling the terminal fibres of

another law in optics that rays of light impinging upon a convex transparent surface, are refracted towards the centre, those being most refracted which are farthest from the centre of the convex surface.

Behind the cornea is a space containing a thin watery fluid, the *aqueous humour*, holding in solution a small quantity of chloride of sodium and extractive matter. The space containing the aqueous humour is divided into an anterior and posterior *chamber* by a membranous partition, *the iris*, to be presently again mentioned. The effect produced by the aqueous humour on the rays of light traversing it, is not yet fully ascertained. Its chief use, probably, is to assist in filling the eyeball, so as to maintain its proper convexity, and at the same time to furnish a medium in which the movements of the iris can take place.

Behind the aqueous humour and the iris, and imbedded in the anterior part of the medium next to be described, viz., the vitreous humour, is seated a doubly-convex body, the *crystalline lens*, which is the most important refracting structure of the eye. The structure of the lens is very complex. It consists essentially of fibres united side by side to each other, and arranged together in very numerous laminæ, which are so placed upon one another, that when hardened in spirit the lens splits into three portions, in the form of sectors, each of which is composed of superimposed concentric laminæ. The lens increases in density and, consequently, in power of refraction, from without inwards; the central

Fig. 183.*



* Fig. 183. Laminated structure of the crystalline lens (from Arnold). *.—The laminæ are split up after hardening in alcohol. 1, the denser central part or nucleus; 2, the successive external layers.

part, usually termed the nucleus, being the most dense. The density of the lens increases with age; it is comparatively soft in infancy, but very firm in advanced life: it is also more spherical at an early period of life than in old age.

The *vitreous humour* constitutes nearly four-fifths of the whole globe of the eye. It fills up the space between the retina and the lens, and its soft jelly-like substance consists essentially of numerous layers, formed of delicate, simple membrane, the spaces between which are filled with a watery, pellucid fluid. It probably exercises some share in refracting the rays of light to the retina; but its principal use appears to be that of giving the proper distension to the globe of the eye, and of keeping the surface of the retina at a proper distance from the lens.

As already observed, the space occupied by the aqueous humour is divided into two portions by a vertically-placed membranous diaphragm, termed the *iris*, provided with a central aperture, the *pupil*, for the transmission of light. The iris is composed of organic muscular fibres imbedded in ordinary fibro-cellular or connective tissue. The muscular fibres of the iris have a direction, for the most part, radiating from the circumference towards the pupil; but as they approach the pupillary margin, they assume a circular direction, and at the very edge form a complete ring. By the contraction of the radiating fibres, the size of the pupil is enlarged: by the contraction of the circular ones, which resemble a kind of sphincter, it is diminished. The object effected by the movements of the iris, is the regulation of the quantity of light transmitted to the retina; the quantity of which is, *cæteris paribus*, directly proportioned to the size of the pupillary aperture. The posterior surface of the iris is coated with a layer of dark pigment, so that no rays of light can pass to the retina, except such as are admitted through the aperture of the pupil.

The *ciliary muscle* is composed of organic muscular fibres, which form a narrow zone around the interior of the eye-ball, near the line of junction of the cornea with the sclerotic, and just behind the outer border of the iris (fig. 178). The *outermost* fibres of this muscle are attached in front to the inner part of the sclerotic and cornea at their line of junction, and, diverging somewhat, are fixed to the ciliary processes, and a small portion of the choroid immediately behind them. The *inner* fibres, immediately within the preceding, form a circular zone around the interior of the eye-ball, outside the ciliary processes. They compose the ring formerly called the ciliary ligament.

The function of this muscle is to adapt the eye for seeing objects at various distances. The manner in which it effects this object will be considered afterwards (p. 650).

The contents of the ball of the eye are surrounded and kept in position by the *cornea*, and the dense, fibrous membrane before referred to as the *sclerotic*, which, besides thus encasing the contents of the eye, serves to give attachment to the various muscles by which the movements of the eye-ball are effected. These muscles, and the nerves supplying them, have been already considered (p. 539, *et seq.*).

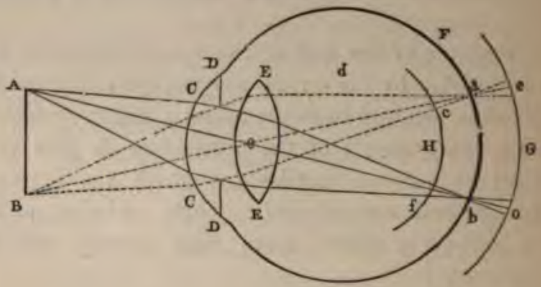
Of the Phenomena of Vision.

The essential constituents of the optical apparatus of the eye may be thus enumerated:—a nervous structure to receive and transmit to the brain the impressions of light; certain refracting media for the purpose of so disposing of the rays of light traversing them as to throw a correct image of an external body on the retina; a contractile diaphragm with a central aperture for regulating the quantity of light admitted into the eye; and a contractile structure by which the chief refracting medium shall be so

controlled as to enable objects to be seen at various distances.

With the help of the diagram below (fig. 184), representing a vertical section of the eye from before backwards, the mode in which, by means of the refracting media of the eye, an image of an object of sight is thrown on the retina, may be rendered intelligible. The rays of the cones of light emitted by the points A B, and every other point of an object placed before the eye, are first refracted, that is, are bent towards the axis of the cone, by the cornea C C, and the aqueous humour contained between it and the lens. The rays of each cone are again refracted

Fig. 184.*



and bent still more towards its central ray or axis by the anterior surface of the lens E E; and again as they pass out through its posterior surface into the less dense medium of the vitreous humour. For a lens has the power of refracting and causing the convergence of the rays of a cone of light, not only on their entrance from a rarer medium into its anterior convex surface, but also at their exit from its posterior convex surface into the rarer medium.

In this manner the rays of the cones of light issuing from the points A and B are again collected to points at *a*

and *b*; and, if the retina F be situated at *a* and *b*, perfect, though reversed, images of the points A and B will be perceived: but if the retina be not at *a* and *b*, but either before or behind that situation,—for instance, at H or G,—circular luminous spots *c* and *f*, or *e* and *o*, instead of points, will be seen; for at H the rays have not yet met, and at G they have already intersected each other, and are again diverging. The retina must therefore be situated at the proper focal distance from the lens, otherwise a defined image will not be formed; or, in other words, the rays emitted by a given point of the object will not be collected into a corresponding point of focus upon the retina.

The means by which *distinct* and *correct* images of objects are formed in the retina, in the various conditions in which the eye is placed in relation to external objects, may be separately considered under the following heads:—1, the means for preventing indistinctness from aberration; 2, the means for preventing it when objects are viewed at different distances; 3, the means by which the *reversed image* of an object on the retina is perceived as in its right position by the mind.

1. Since the retina is concave, and from its centre towards its margins gradually approaches the lens, it follows that the images of objects situated at the sides cannot be so distinct as those of objects nearer to the middle of the field of vision, and of which the images are formed at a distance beyond the lens exactly corresponding to the situation of the retina. Moreover, the rays of a cone of light from an object situated at the side of the field of vision do not meet all in the same point, owing to their unequal refraction; for the refraction of the rays which pass through the circumference of a lens is greater than that of those traversing its central portion. The concurrence of these two circumstances would cause indistinctness of vision, unless corrected by some contrivance. Such

correction is effected, in both cases, by the iris, which forms a kind of annular diaphragm to cover the circumference of the lens, and to prevent the rays from passing through any part of the lens but its centre, which corresponds to the pupil.

The image of an object will be most defined and distinct when the pupil is narrow, the object at the proper distance for vision, and the light abundant; so that, while a sufficient number of rays are admitted, the narrowness of the pupil may prevent the production of indistinctness of the image by this *spherical aberration* or unequal refraction just mentioned. But even the image formed by the rays passing through the circumference of the lens, when the pupil is much dilated, as in the dark, or in a feeble light, may, under certain circumstances, be well defined; the image formed by the central rays being then indistinct or invisible, in consequence of the retina not receiving these rays where they are concentrated to a focus.

Distinctness of vision, is further secured by the inner surface of the choroid, immediately external to the retina itself, as well as the posterior surface of the iris and the ciliary processes, being coated with black pigment, which absorbs any rays of light that may be reflected within the eye, and prevents their being thrown again upon the retina so as to interfere with the images there formed. The pigment of the choroid is especially important in this respect; for the retina is very transparent, and if the surface behind it were not of a dark colour, but capable of reflecting the light, the luminous rays which had already acted on the retina would be reflected again through it, and would fall upon other parts of the same membrane, producing both dazzling from excessive light, and indistinctness of the images.

In the passage of light through an ordinary convex lens, decomposition of each ray into its elementary coloured parts commonly ensues, and a coloured margin appears

around the image, owing to the unequal refraction which the elementary colours undergo. In the optical instruments this, which is termed *chromatic aberration*, is corrected by the use of two or more lenses, differing in shape and density, the second of which continues or increases the refraction of the rays produced by the first, but by recombining the individual parts of each ray into its original white light, corrects any chromatic aberration which may have resulted from the first. It is probable that the unequal refractive power of the transparent media in front of the retina may be the means by which the eye is enabled to guard against the effect of chromatic aberration. The human eye is achromatic, however, only so long as the image is received at its focal distance upon the retina, or so long as the eye adapts itself to the different distances of sight. If either of these conditions be interfered with, a more or less distinct appearance of colours is produced.

2. The distinctness of the image formed upon the retina is mainly dependent on the rays emitted by each luminous point of the object being brought to a perfect focus upon the retina. If this focus occur at a point either in front of, or behind the retina, indistinctness of vision ensues, with the production of a halo. The *focal distance, i.e.*, the distance of the point at which the luminous rays from a lens are collected, besides being regulated by the degree of convexity and density of the lens, varies with the distance of the object from the lens, being greater as this is shorter, and *vice versâ*. Hence, since objects placed at various distances from the eye can, within a certain range, different in different persons, be seen with almost equal distinctness, there must be some provision by which the eye is enabled to adapt itself, so that whatever length the focal distance may be, the focal point may always fall exactly upon the retina.

This power of *adaptation of the eye to vision at different distances* has received the most varied explanations. It is

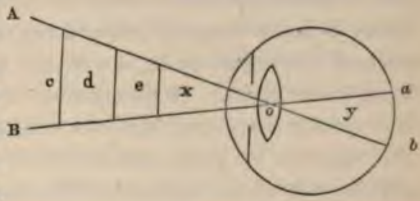
obvious that the effect might be produced in either of two ways, viz., by altering the convexity or density, and thus the refracting power, either of the cornea or lens; or, by changing the position either of the retina or of the lens, so that whether the object viewed be near or distant, and the focal distance thus increased or diminished, the focal point to which the rays are converged by the lens may always be at the place occupied by the retina. The amount of either of these changes required in even the widest range of vision, is extremely small. For, from the refractive powers of the media of the eye, it has been calculated by Olbers, that the difference between the focal distances of the images of an object at such a distance that the rays are parallel, and of one at the distance of four inches, is only about 0.143 of an inch. On this calculation, the change in the distance of the retina from the lens required for vision at all distances, supposing the cornea and lens to maintain the same form, would not be more than about one line.

It is now almost universally believed that Helmholtz is right in his statement that the immediate cause of the adaptation of the eye for objects at different distances is a varying shape of the lens, its front surface becoming more or less convex, according to the distance of the object looked at. The nearer the object, the more convex does the front surface of the lens become, and *vice versâ;* the back surface taking little or no share in the production of the effect required. Of course, the lens has no inherent power of contraction, and therefore its changes of outline must be produced by some power from without; and there seems no reason to doubt that this power is supplied by the ciliary muscle. The exact manner, however, in which, by its contraction, the ciliary muscle effects a change in the shape of the crystalline lens is doubtful. The most probable explanation of the phenomenon, however, is that in adapting the eye for viewing near objects the ciliary

muscle contracts, and, by such contraction, diminishes the force with which the elastic suspensory ligament of the lens is tending to flatten it. On the latter supposition, the lens may be supposed to be always in a state of tension and partial flattening from the action of the suspensory ligament; while the ciliary muscle, by diminishing the tension of this ligament, diminishes, to a proportional degree, the flattening of which it is the cause. On diminution or cessation of the action of the ciliary muscle, the lens returns, in a corresponding degree, to its former shape, by virtue of the elasticity of its suspensory ligament. In viewing near objects, the iris contracts, so that its pupillary edge is moved a very little forwards, and the pupil itself is contracted—the opposite effect taking place on withdrawal of the attention from near objects, and fixing it on those distant.

The range of distances through which persons can adapt their power of vision is not in all cases the same. Some persons possess scarcely any power of adaptation, and of this defect of vision there are two kinds; one, in which the person can see objects distinctly only when brought close to the eye, having little power to discern distant objects; another, in which distant objects alone can be distinctly perceived, a small body being almost invisible except when held at a considerable distance from the eye. In the one case the person is said to be short-sighted or myopic: in the other, long-sighted or presbyopic. Myopia is caused by anything, such as undue convexity of the lens, which increases the refracting power of the eye, and so causes the image of the object

Fig. 185.*



to be formed at a point anterior to the retina: the defect is remedied by the use of concave glasses. Presbyopia, or long-sightedness, is the result of conditions the reverse of the above, and is remedied by the use of convex glasses, which diminish the focal distance of an image formed in the eye.*

3. The direction given to the rays by their refraction is regulated by that of the central ray, or axis of the cone, towards which the rays are bent. The image of any point of an object is, therefore, as a rule (the exceptions to which need not here be stated), always formed in a line identical with the axis of the cone of light, as in the line of B *a*, or A *b*, fig. 185: so that the spot where the image of any point will be formed upon the retina may be determined by prolonging the central ray of the cone of light, or that ray which traverses the centre of the pupil. Thus A *b* is the axis or central ray of the cone of light issuing from A; B *a*, the central ray of the cone of light issuing from B; the image of A is formed at *b*, the image of B at *a*, in the inverted position; therefore what in the object was above is in the image below, and *vice versâ*,—the right-hand part of the object is in the image to the left, the left-hand to the right. If an opening be made in an eye at its superior surface, so that the retina can be seen through the vitreous humour, this reversed image of any bright object, such as the windows of the room, may be perceived at the bottom of the eye. Or still better, if the eye of any albino animal, such as a white rabbit, in which the coats, from the absence of pigment, are transparent, is dissected clean, and held with the cornea towards a window, a very distinct image of the window completely inverted is seen depicted on the posterior translucent wall of the eye. Volkmann has also shown that a similar experiment may

* For details on this subject, consult the various treatises on the Physiology and Defects of Vision.

be successfully performed in a living person possessed of large prominent eyes, and an unusually transparent sclerotica.

No completely satisfactory explanation has yet been offered to account for the mind being able to form a correct idea of the erect position of an object of which an inverted image is formed on the retina. Müller and Volkmann are of opinion that the mind really perceives an object as inverted, but needs no correction, since everything is seen alike inverted, and the relative position of the objects therefore remains unchanged: and the only proof we can possibly have of the inversion is by experiment and the study of the laws of optics. It is the same thing as the daily inversion of objects consequent on the revolution of the entire earth, which we know only by observing the position of the stars; and yet it is certain that, within twenty-four hours, that which was below in relation to the stars, comes to be above. Hence it is, also, that no discordance arises between the sensations of inverted vision and those of touch, which perceives everything in its erect position; for the images of all objects, even of our own limbs, in the retina, are equally inverted, and therefore maintain the same relative position. Even the image of our hand, while used in touch, is seen inverted. The position in which we see objects, we call therefore the erect position. A mere lateral inversion of our body in a mirror, where the right hand occupies the left of the image, is indeed scarcely remarked: and there is but little discordance between the sensations acquired by touch in regulating our movements by the image in the mirror, and those of sight, as, for example, in tying a knot in the cravat. There is some want of harmony here, on account of the inversion being only lateral, and not complete in all directions.

The perception of the erect position of objects appears, therefore, to be the result of an act of the mind. And this

leads us to a consideration of the several other properties of the retina, and of the co-operation of the mind in the several other parts of the act of vision. To these belong not merely the act of sensation itself, and the perception of the changes produced in the retina, as light and colours, but also the conversion of the mere images depicted in the retina into ideas of an extended field of vision, of proximity and distance, of the form and size of objects, of the reciprocal influence of different parts of the retina upon each other, the simultaneous action of the two eyes, and some other phenomena.

To speak first of the *ideal size of the field of vision* :—The actual size of the field of vision depends on the extent of the retina, for only so many images can be seen at any one time as can occupy the retina, at the same time; and thus considered, the retina, of which the affections are perceived by the mind, is itself the field of vision. But to the mind of the individual the size of the field of vision has no determinate limits; sometimes it appears very small, at another time very large; for the mind has the power of projecting the images on the retina towards the exterior. Hence the mental field of vision is very small when the sphere of the action of the mind is limited to impediments near the eye: on the contrary, it is very extensive when the projection of the images on the retina towards the exterior, by the influence of the mind, is not impeded. It is very small when we look into a hollow body of small capacity held before the eyes; large when we look out upon the landscape through a small opening; more extensive when we look at the landscape through a window; and most so when our view is not confined by any near object. In all these cases the idea which we receive of the size of the field of vision is very different, although its absolute size is in all the same, being dependent on the extent of the retina. Hence it follows, that the mind is constantly co-operating in the acts of vision, so that at last

it becomes difficult to say what belongs to mere sensation, and what to the influence of the mind.

By a mental operation of this kind, we obtain a correct idea of the size of individual objects, as well as of the extent of the field of vision. To understand this, it will be necessary to refer again to fig. 185, p. 651.

The angle x, included between the decussating central rays of two cones of light issuing from different points of an object, is called the optical angle—*angulus opticus seu visorius*. This angle becomes larger, the greater the distance between the points A and B; and since the angles x and y are equal, the distance between the points a and b in the image on the retina increases as the angle x becomes larger. Objects at different distances from the eye, but having the same optical angle, x—for example, the objects, c, d, and e,—must also throw images of equal size upon the retina; and, if they occupy the same angle of the field of vision, their image must occupy the same spot in the retina.

Nevertheless, these images appear to the mind to be of very unequal size when the ideas of distance and proximity come into play; for, from the image a b, the mind forms the conception of a visual space extending to e, d, or c, and of an object of the size which that represented by the image on the retina appears to have when viewed close to the eye, or under the most usual circumstances. A landscape depicted on the retina, as a b, and viewed under the angle x, is therefore conceived by the mind to have an extent of two miles perhaps, if we know that its extent is such, or if we infer it to be so from the number of known objects seen at the same time. And in the same way that the images of several different objects, viewed under the same angle, thus appears to the mind to have a different size in the field of vision, so the whole field of vision, which has always the same absolute size, is interpreted by the mind as of extremely various extent: and, for this reason

also, the image viewed in the camera obscura is regarded as a real landscape—as the true field of vision—although only a small image depicted upon paper. The same mental process gives rise to the idea of depth in the field of vision; this idea being fixed in our mind principally by the circumstance that, as we ourselves move forwards, different images in succession become depicted on our retina, so that we seem to pass between these images, which to the mind is the same thing as passing between the objects themselves.

The action of the sense of vision in relation to external objects is, therefore, quite different from that of the sense of touch. The objects of the latter sense are immediately present to it; and our own body, with which they come into contact, is the measure of their size. The part of a table touched by the hand appears as large as the part of the hand receiving an impression from it, for a part of our body in which a sensation is excited is here the measure by which we judge of the magnitude of the object. In the sense of vision, on the contrary, the images of objects are mere fractions of the objects themselves realized upon the retina, the extent of which remains constantly the same. But the imagination, which analyzes the sensations of vision, invests the images of objects, together with the whole field of vision in the retina, with very varying dimensions; the relative size of the images in proportion to the whole field of vision, or of the affected parts of the retina to the whole retina, alone remaining unaltered.

The direction in which an object is seen, the *direction of vision*, or *visual direction*, depends on the part of the retina which receives the image, and on the distance of this part from, and its relation to, the central point of the retina. Thus, objects of which the images fall upon the same parts of the retina lie in the same visual direction; and when, by the action of the mind, the images or affections of the

retina are projected into the exterior world, the relation of the images to each other remains the same.

The estimation of the *form of bodies* by sight is the result partly of the mere sensation, and partly of the association of ideas. Since the form of the images perceived by the retina depends wholly on the outline of the part of the retina affected, the sensation alone is adequate to the distinction of only superficial forms of each other, as of a square from a circle. But the idea of a solid body, as a sphere, or a body of three or more dimensions, *e.g.*, a cube, can only be attained by the action of the mind constructing it from the different superficial images seen in different positions of the eye with regard to the object; and, as shown by Mr. Wheatstone and illustrated in the stereoscope, from two different perspective projections of the body being presented simultaneously to the mind by the two eyes. Hence, when, in adult age, sight is suddenly restored to persons blind from infancy, all objects in the field of vision appear at first as if painted flat on one surface; and no idea of solidity is formed until after long exercise of the sense of vision combined with that of touch.

We judge of the *motion* of an object, partly from the motion of its image over the surface of the retina, and partly from the motion of our eyes following it. If the image upon the retina moves while our eyes and our body are at rest, we conclude that the object is changing its relative position with regard to ourselves. In such a case the movement of the object may be apparent only, as when we are standing upon a body which is in motion, such as a ship. If, on the other hand, the image does not move with regard to the retina, but remains fixed upon the same spot of that membrane, while our eyes follow the moving body, we judge of the motion of the object by the sensation of the muscles in action to move the eye. If the image moves over the surface of the retina while the mus-

cles of the eye are acting at the same time in a manner corresponding to this motion, as in reading, we infer that the object is stationary, and we know that we are merely altering the relations of our eyes to the object. Sometimes the object appears to move when both object and eye are fixed, as in vertigo.

The mind can, by the faculty of *attention*, concentrate its activity more or less exclusively upon the senses of sight, hearing, and touch alternately. When exclusively occupied with the action of one sense, it is scarcely conscious of the sensations of the others. The mind, when deeply immersed in contemplations of another nature, is indifferent to the actions of the sense of sight, as of every other sense. We often, when deep in thought, have our eyes open and fixed, but see nothing, because of the stimulus of ordinary light being unable to excite the mind to perception when otherwise engaged. The attention which is thus necessary for vision, is necessary also to analyse what the field of vision presents. The mind does not perceive all the objects presented by the field of vision at the same time with equal acuteness, but directs itself first to one and then to another. The sensation becomes more intense, according as the particular object is at the time the principal object of mental contemplation. Any compound mathematical figure produces a different impression according as the attention is directed exclusively to one or the other part of it. Thus, in fig. 186, we may in succession have a vivid perception of the whole, or of distinct parts only; of the six triangles near the outer circle, of the hexagon in the middle, or of the three large triangles. The more numerous and varied the parts of which a figure is composed, the more scope does it afford for the play of the attention. Hence it is that architectural ornaments have an enlivening effect on

Fig. 186.

the sense of vision, since they afford constantly fresh subject for the action of the mind.

The *duration* of the sensation produced by a luminous impression on the retina is always greater than that of the impression which produces it. However brief the luminous impression, the effect on the retina always lasts for about one-eighth of a second. Thus, supposing an object in motion, say a horse, to be revealed on a dark night by a flash of lightning. The object would be seen apparently for an eighth of a second, but it would not appear in motion; because although the image remained on the retina for this time, it was really revealed for such an extremely short period (the duration of a flash of lightning being almost instantaneous) that no appreciable movement on the part of the object could have taken place in the period during which it was revealed to the retina of the observer. And the same fact is proved in a reverse way. The spokes of a rapidly revolving wheel are not seen as distinct objects, because at every point of the field of vision over which the revolving spokes pass, a given impression has not faded before another comes to replace it. Thus every part of the interior of the wheel appears occupied.

The duration of the *after-sensation* or *spectrum*, produced by an object, is greater in a direct ratio with the duration of the impression which caused it. Hence the image of a bright object, as of the panes of a window through which the light is shining, may be perceived in the retina for a considerable period, if we have previously kept our eye fixed for some time on it.

The colour of the spectrum varies with that of the object which produced it. The spectra left by the images of white or luminous objects, are ordinarily white or luminous; those left by dark objects are dark. Sometimes, however, the relation of the light and dark parts in the image may, under certain circumstances, be reversed in the spectrum; what was bright may be dark, and what

was dark may appear light. This occurs whenever the eye, which is the seat of the spectrum of a luminous object, is not closed, but fixed upon another bright or white surface, as a white wall, or a sheet of white paper. Hence the spectrum of the sun, which, while light is excluded from the eye is luminous, appears black or grey when the eye is directed upon a white surface. The explanation of this is, that the part of the retina which has received the luminous image remains for a certain period afterwards in an exhausted or less sensitive state, while that which has received a dark image is in an unexhausted, and therefore much more excitable condition.

Fig. 187.*

The ocular spectra which remain after the impression of coloured objects upon the retina are always coloured; and

* Fig. 187. A circle showing the various simple and compound colours of light, and those which are complemental of each other, *i.e.*, which, when mixed, produce a neutral grey tint. The three simple colours, red, yellow, and blue, are placed at the angles of an equilateral triangle; which are connected together by means of a circle; the mixed colours, green, orange, and violet, are placed intermediate between the corresponding simple or homogeneous colours; and the complemental colours, of which the pigments, when mixed, would constitute a grey, and of which the prismatic spectra would together produce a white light, will be found to be placed in each case opposite to each other, but connected by a line passing through the centre of the circle. The figure is also useful in showing the further shades of colour which are complementary of each other. If the circle be supposed to contain every transition of colour between the six marked down, those which, when united, yield a white or grey colour, will always be found directly opposite to each other; thus, for example, the intermediate tint between orange and red is complemental of the middle tint between green and blue.

their colour is not that of the object, or of the image produced directly by the object, but the opposite, or *complemental* colour. The spectrum of a red object is, therefore, green; that of a green object, red; that of violet, yellow; that of yellow, violet, and so on. The reason of this is obvious. The part of the retina which receives, say, a red image, is wearied by that particular colour, but remains sensitive to the other rays which with red make up white light; and, therefore, these by themselves reflected from a white object produce a green hue. If, on the other hand, the first object looked at be green, the retina being tired of green rays, receives a red image when the eye is turned to a white object. And so with the other colours; the retina while fatigued by yellow rays will suppose an object to be violet, and *vice versâ;* the size and shape of the spectrum corresponding with the size and shape of the original object looked at. The colours which thus reciprocally excite each other in the retina are those placed at opposite points of the circle in fig. 187.

Of the Reciprocal Action of different Parts of the Retina on each other.

Although each elementary part of the retina represents a distinct portion of the field of vision, yet the different elementary parts, or sensitive points, of that membrane have a certain influence on each other; the particular condition of one influencing that of another, so that the image perceived by one part is modified by the image depicted in the other. The phenomena, which result from this relation between the different parts of the retina, may be arranged in two classes; the one including those where the condition existing in the greater extent of the retina is imparted to the remainder of that membrane; the other, consisting of those in which the condition of the larger portion of the retina excites, in the less extensive portion, the opposite condition.

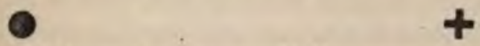
1. When two opposite impressions occur in contiguous parts of an image on the retina, the one impression is, under certain circumstances, modified by the other. If the impressions occupy each one-half of the image, this does not take place; for in that case, their actions are equally balanced. But if one of the impressions occupies only a small part of the retina, and the other the greater part of its surface, the latter may, if long continued, extend its influence over the whole retina, so that the opposite less extensive impression is no longer perceived, and its place becomes occupied by the same sensation as the rest of the field of vision. Thus, if we fix the eye for some time upon a strip of coloured paper lying upon a white surface, the image of the coloured object, especially when it falls on the lateral parts of the retina, will gradually disappear, and the white surface be seen in its place.

2. In the second class of phenomena, the affection of one part of the retina influences that of another part, not in such a manner as to obliterate it, but so as to cause it to become the contrast or opposite of itself. Thus a grey spot upon a white ground appears darker than the same tint of grey would do if it alone occupied the whole field of vision, and a shadow is always rendered deeper when the light which gives rise to it becomes more intense, owing to the greater contrast. The former phenomena ensue gradually, and only after the images have been long fixed on the retina; the latter are instantaneous in their production, and are permanent.

In the same way, also, colours may be produced by contrast. Thus, a very small dull-grey strip of paper, lying upon an extensive surface of any bright colour, does not appear grey, but has a faint tint of the colour which is the complement of that of the surrounding surface (see page 661). A strip of grey paper upon a green field, for example, often appears to have a tint of red, and when

lying upon a red surface, a greenish tint; it has an orange-coloured tint upon a bright blue surface, and a blueish tint upon an orange-coloured surface; a yellowish colour upon a bright violet, and a violet tint upon a bright yellow surface. The colour excited thus, as a contrast to the exciting colour, being wholly independent of any rays of the corresponding colour acting from without upon the retina, must arise as an opposite or antagonistic condition of that membrane; and the opposite conditions of which the retina thus becomes the subject would seem to balance each other by their reciprocal reaction. A necessary condition for the production of the contrasted colours is, that the part of the retina in which the new colour is to be excited, shall be in a state of comparative repose; hence the small object itself must be grey. A second condition is, that the colour of the surrounding surface shall be very bright, that is, it shall contain much white light.

The retina corresponding to the point of entrance of the optic nerve is completely insensible to the impressions of light. The phenomenon itself is very readily shown. If we direct one eye, the other being closed, upon a point at such a distance to the side of any object, that the image of the latter must fall upon the retina at the point of entrance of the optic nerve, this image is lost either



instantaneously, or very soon. If, for example, we close the left eye, and direct the axis of the right eye steadily towards the circular spot here represented, while the page is held at a distance of about six inches from the eye, both dot and cross are visible. On gradually increasing the distance between the eye and the object, by removing the book farther and farther from the face, and still keeping the right eye steadily on the dot, it will be found that suddenly the cross disappears from view, while on removing the book still farther, it suddenly comes in sight

again. The cause of this phenomenon is simply that the portion of retina which is occupied by the entrance of the optic nerve, is quite blind; and therefore that when it alone occupies the field of vision, objects cease to be visible.

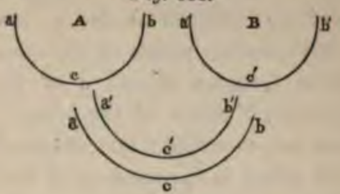
Of the Simultaneous Action of the two Eyes.

Although the sense of sight is exercised by two organs, yet the impression of an object conveyed to the mind is single. Various theories have been advanced to account for this phenomenon. By Gall, it was supposed that we do not really employ both eyes simultaneously in vision, but always see with only one at a time. This especial employment of one eye in vision certainly occurs in persons whose eyes are of very unequal focal distance, but in the majority of individuals both eyes are simultaneously in action in the perception of the same object; this is shown by the double images seen under certain conditions. If two fingers be held up before the eyes, one in front of the other, and vision be directed to the more distant, so that it is seen singly, the nearer will appear double; while, if the nearer one be regarded, the most distant will be seen double; and one of the double images in each case will be found to belong to one eye, the other to the other eye.

Single vision results only when certain parts of the two retinæ are affected simultaneously; if different parts of the retinæ receive the image of the object, it is seen double. The parts of the retinæ in the two eyes which thus correspond to each other in the property of referring the images which affect them simultaneously to the same spot in the field of vision are, in man, just those parts which would correspond to each other, if one retina were placed exactly in front of, and over the other (as in fig. 188, c). Thus, the outer lateral portion of one eye corresponds to, or, to use a better term, is identical with,

the inner portion of the other eye; or *a* of the eye A (fig. 188) with *a′* of the eye B. The upper part of one retina is also identical with the upper part of the other; and the lower parts of the two eyes are identical with each other.

Fig. 188.



This is proved by a single experiment. Pressure upon any part of the ball of the eye, so as to affect the retina, produces a luminous circle, seen at the opposite side of the field of vision to that on which the pressure is made. If, now, in a dark room, we press with the finger at the upper part of one eye, and at the lower part of the other, two luminous circles are seen, one above the other; so, also, two figures are seen when pressure is made simultaneously on the two outer or the two inner sides of both eyes. It is certain, therefore, that neither the upper part of one retina and the lower part of the other are identical, nor the outer lateral parts of the two retinæ, nor their inner lateral portions. But if pressure be made with the fingers upon both eyes simultaneously at their lower part, one luminous ring is seen at the middle of the upper part of the field of vision; if the pressure be applied to the upper part of both eyes, a single luminous circle is seen in the middle of the field of vision below. So, also, if we press upon the outer side *a* of the eye A, and upon the inner side *a′* of the eye B, a single spectrum is produced, and is apparent at the extreme right of the field of vision; if upon the point *b* of one eye, and the point *b′* of the other, a single spectrum is seen to the extreme left.

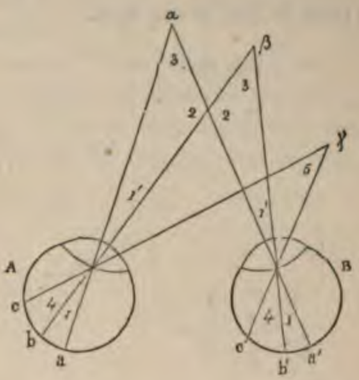
The spheres of the two retinæ may, therefore, be regarded as lying one over the other, as in C, fig. 188; so that the left portion of one eye lies over the identical left portion of the other eye, the right portion of one eye over

the identical right portion of the other eye; and with the upper and lower portions of the two eyes, a lies over a', b over b', and c over c'. The points of the one retina intermediate between a and c, are again identical with the corresponding points of the other retina between a' and c'; those between b and c of the one retina, with those between b' and c' of the other. In short, all other parts are non-identical: and, when they are excited to action, the effect is the same as if the impressions were made on different parts of the same retina: and the double images belonging to the eyes A and B, are seen at exactly the same distance from each other as exists between the image of the eye A and the part of the retina of the eye A which corresponds to, or is identical with, the seat of the second image in the eye B; or, to return to the figure already used in illustration (fig. 188), if a of one eye be affected, and b' of the other, the distances of the two images a and b' will, inasmuch as a is identical with a', and b' with b, lie at exactly the same distance from each other as images produced by impressions on the points a b of the one eye, or a' b' of the other.

In application of these results to the phenomena of vision, if the position of the eyes with regard to a luminous object be such that similar images of the same object fall on identical parts of the two retinæ, as occurs when the axes meet in some one point, the object is seen single; if otherwise, as in the various forms of squinting, two images are formed, and double vision results. If the axes of the eyes, A and B (fig. 189), be so directed that they meet at a, an object at a, will be seen singly, for the point a of the one retina, and a' of the other, are identical. So, also, if the object β be so situated that its image falls in both eyes at the same distance from the central point of the retina, —namely, at b in the one eye, and at b' in the other,—β will be seen single, for it affects identical parts of the two retinæ. The same will apply to the object γ'.

In quadrupeds, the relation between the identical and non-identical parts of the retinæ cannot be the same as in man; for the axes of their eyes generally diverge, and can never be made to meet in one point of an object. When an animal regards an object situated directly in front of it, the image of the object must fall, in both eyes, on the outer portion of the retinæ. Thus the image of the object

Fig. 189.



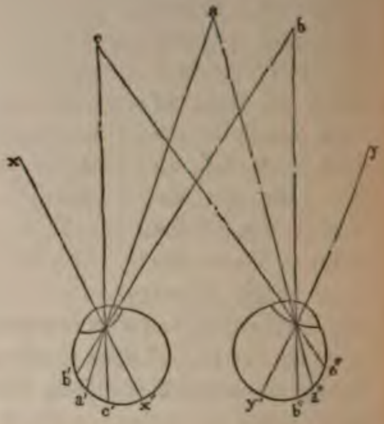
a (fig. 191) will fall at *a′* in one, and at *a″* in the other: and these points *a′* and *a″* must be identical. So, also, for distinct and single vision of objects, *b* or *c*, the points *b′* and *b″*, or *c′ c″*, in the two retinæ, on which the images of these objects fall, must be identical. All points of the retina in each eye which receive rays of light from lateral objects only, can have no corresponding identical points in the retina of the other eye; for otherwise two objects, one situated to the right and the other to the left, would appear to lie in the same spot of the field of vision. It is probable, therefore, that there are, in the eyes of animals, parts of the retinæ which are identical, and parts which are not identical, *i.e.*, parts in one which have no corresponding parts in the other eye. And the relation of the two retinæ to each other in the field of vision may be represented as in fig. 190.

The cause of the impressions on the identical points of the two retinæ giving rise to but one sensation, and the perception of a single image, must either lie in the structure

tural organization of the deeper or cerebral portion of the visual apparatus, or be the result of a mental operation; for in no other case is it the property of the corresponding nerves of the two sides of the body to refer their sensations as one to one spot.

Fig. 190.

Fig. 191.



Many attempts have been made to explain this remarkable relation between the eyes, by referring it to anatomical relation between the optic nerves. The circumstance of the inner portion of the fibres of the two optic nerves decussating at the commissure, and passing to the eye of the opposite side, while the outer portion of the fibres continue their course to the eye of the same side, so that the left side of both retinæ is formed from one root of the nerves, and the right side of both retinæ from the other root, natually lead to an attempt to explain the phenomenon by this distribution of the fibres of the nerves. And this explanation is favoured by cases in which the entire of one side of the retina, as far as the central point in both eyes, sometimes becomes insensible. But Müller shows the inadequateness of this theory to explain the

phenomenon, unless it be supposed that each fibre in each cerebral portion of the optic nerves divides in the optic commissure into two branches for the identical points of the two retinæ, as is shown in fig. 192. But there is no foundation for such supposition.

By another theory it is assumed that each optic nerve contains exactly the same number of fibres as the other, and that the corresponding fibres of the two nerves are united in the sensorium (as in fig. 193). But in this

Fig. 192.

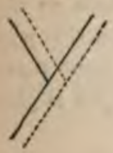


Fig. 193.

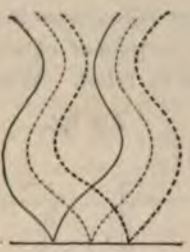
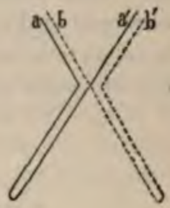


Fig. 194.



theory no account is taken of the partial decussation of the fibres of the nerves in the optic commissure.

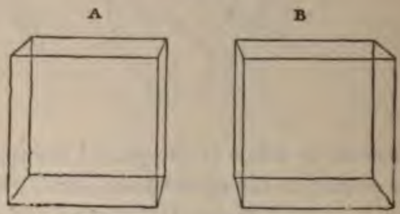
According to a third theory, the fibres *a* and *a'*, fig. 194, coming from identical points of the two retinæ, are in the optic commissure brought into one optic nerve, and in the brain either are united by a loop, or spring from the same point. The same disposition prevails in the case of the identical fibres *b* and *b'*. According to this theory, the left half of each retina would be represented in the left hemisphere of the brain, and the right half of each retina in the right hemisphere.

Another explanation is founded on the fact, that at the anterior part of the commissure of the optic nerve, certain fibres pass across from the distal portion of one nerve to the corresponding portion of the other nerves, as if they were commissural fibres forming a connection between the

retinæ of the two eyes. It is supposed, indeed, that these fibres may connect the corresponding parts of the two retinæ, and may thus explain their unity of action; in the same way that corresponding parts of the cerebral hemispheres are believed to be connected together by the commissural fibres of the corpus callosum, and so enabled to exercise unity of function.

But, on the whole, it is more probable, that the power of forming a single idea of an object from a double impression conveyed by it to the eyes is the result of a mental act. This view is supported by the same facts as those employed by Professor Wheatstone to show that this power is subservient to the purpose of obtaining a right perception of bodies raised in relief. When an object is placed

Fig. 195.



so near the eyes that to view it the optic axes must converge, a different perspective projection of it is seen by each eye, these perspectives being more dissimilar as the convergence of the optic axes becomes greater. Thus, if any figure of three dimensions, an outline cube, for example, be held at a moderate distance before the eyes, and viewed with each eye successively, while the head is kept perfectly steady, A (fig. 195) will be the picture presented to the right eye, and B that seen by the left eye. Mr. Wheatstone has shown that on this circumstance depends in a great measure our conviction of the solidity of an object, or of its projection in relief. If different perspective drawings of a solid body, one representing the

image seen by the right eye, the other that seen by the left (for example, the drawing of a cube A, B, fig. 195), be presented to corresponding parts of the two retinæ, as may be readily done by means of the *stereoscope*, an instrument invented by Professor Wheatstone for the purpose, the mind will perceive not merely a single representation of the object, but a body projecting in relief, the exact counterpart of that from which the drawings were made.

SENSE OF HEARING.

Anatomy of the Organ of Hearing.

For descriptive purposes, the ear, or organ of hearing, is divided into three parts, the *external*, the *middle*, and the *internal* ear. The two first are only accessory to the third or internal ear, which contains the essential parts of an organ of hearing. The accompanying figure shows very well the relation of these divisions,—one to the other (fig. 196).

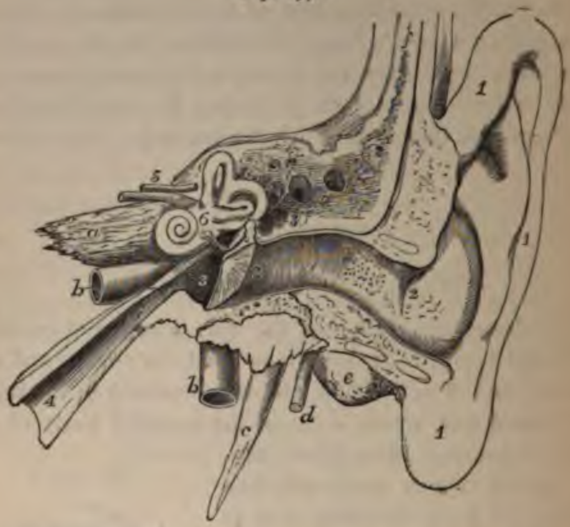
Fig. 196.*

The external ear consists of the *pinna* or *auricle*, and the external *auditory canal* or *meatus*. The principal parts of the *pinna* are two prominent rims enclosed one within the other (*helix* and *antihelix*), and enclosing a central hollow named the *concha;* in front of the concha, a prominence directed backwards, the *tragus*, and opposite to this, one directed forwards, the *antitragus*. From the concha, the

* Fig. 196. Outer surface of the pinna of the right auricle. $\frac{2}{3}$.—1, helix; 2, fossa of the helix; 3, antihelix; 4, fossa of the antihelix; 5, antitragus; 6, tragus; 7, concha; 8, lobule.

auditory canal, with a slight arch directed upwards, passes inwards and a little forwards to the membrana tympani,

Fig. 197.*



to which it thus serves to convey the vibrating air. Its

* Fig. 197. Diagrammatic view from before of the parts composing the organ of hearing of the left side (after Arnold).—The temporal bone of the left side, with the accompanying soft parts, has been detached from the head, and a section has been carried through it transversely, so as to remove the front of the meatus externus, half the tympanic membrane, the upper and anterior wall of the tympanum and Eustachian tube. The meatus internus has also been opened, and the bony labyrinth exposed by the removal of the surrounding parts of the petrous bone. 1, the pinna and lobe; 2, 2′, meatus externus; 2′, membrana tympani; 3, cavity of the tympanum; 3′, its opening backwards into the mastoid cells; between 3 and 3′, the chain of small bones; 4, Eustachian tube; 5, meatus internus containing the facial (uppermost) and the auditory nerves; 6, placed on the vestibule of the labyrinth above the fenestra ovalis: *a*, apex of the petrous bone; *b*, internal carotid artery; *c*, styloid process; *d*, facial nerve issuing from the stylo-mastoid foramen; *e*, mastoid process; *f*, squamous part of the bone covered by integument, etc.

outer part consists of fibro-cartilage continued from the concha; its inner part of bone. Both are lined by skin continuous with that of the pinna, and extending over the outer part of the *membrana tympani.* Towards the outer part of the canal are fine hairs and sebaceous glands, while deeper in the canal are small glands, resembling the sweat-glands in structure, which secrete a peculiar yellow substance called *cerumen,* or ear-wax.

The *middle* ear, or *tympanum* (3, fig. 197) is separated by the *membrana tympani* from the external auditory canal. It is a cavity in the temporal bone, opening through its anterior and inner wall into the Eustachian tube, a cylindriform flattened canal, dilated at both ends, composed partly of bone and partly of cartilage, lined with mucous membrane, and forming a communication between the tympanum and the pharynx. It opens into the cavity of the pharynx just behind the posterior aperture of the nostrils. The cavity of the tympanum communicates posteriorly with air-cavities, the *mastoid cells* in the mastoid process of the temporal bone; but its only opening to the external air is through the Eustachian tube (4, fig. 197). The walls of the tympanum are osseous, except where apertures in them are closed with membrane, as at the fenestra rotunda, and fenestra ovalis, and at the outer part where the bone is replaced by the *membrana tympani.* The cavity of the tympanum is lined with mucous membrane, the epithelium of which is ciliated and continuous with that of the pharynx. It contains a chain of small bones (*ossicula auditus*), which extends from the membrana tympani to the fenestra ovalis.

The *membrana tympani* is placed in a slanting direction at the bottom of the external auditory canal, its plane being at an angle of about 45° with the lower wall of the canal. It is formed chiefly of a tough and tense fibrous membrane, the edges of which are set in a bony groove; its outer surface is covered with a continuation of the

cutaneous lining of the auditory canal, its inner surface with part of the ciliated mucous membrane of the tympanum.

The small bones or *ossicles* of the ear are three, named *malleus*, *incus*, and *stapes*. The *malleus*, or hammer-bone, is attached by a long slightly-curved process, called its handle, to the membrana tympani; the line of attachment being vertical, including the whole length of the handle, and extending from the upper border to the centre of the membrane. The head of the malleus is irregularly rounded; its neck, or the line of boundary between it and the handle, supports two processes; a *short* conical one, which receives the insertion of the *tensor tympani*, and a *slender* one, *processus gracilis*, which extends forwards, and to which the *laxator tympani* muscle is attached. The *incus*, or anvil-bone, shaped like a bicuspid molar tooth, is articulated by its broader part, corresponding with the surface of the crown of a tooth, to the malleus. Of its two fang-like processes, one, directed backwards, has a free end, the other, curved downwards and more pointed, articulates by means of a roundish tubercle, formerly called *os orbiculare*, with the stapes, a little bone shaped exactly like a stirrup, of which the base or bar fits into the fenestra ovalis. To the neck of the stapes, a short process, corresponding with the loop of the stirrup, is attached the *stapedius* muscle.

The bones of the ear are covered with mucous membrane reflected over them from the wall of the tympanum; and are moveable both altogether and one upon the other. The malleus moves and vibrates with every movement and vibration of the membrana tympani, and its movements are communicated through the incus to the stapes, and through it to the membrane closing the fenestra ovalis. The malleus, also, is moveable in its articulation with the incus; and the membrana tympani moving with it is altered in its degree of tension by the laxator and tensor

tympani muscles. The stapes is moveable on the process of the incus, when the stapedius muscle acting draws it backwards.

The proper organ of hearing is formed by the distribution of the auditory nerve within the *internal ear*, or *labyrinth* of the ear, a set of cavities within the petrous portion of the temporal bone. The bone which forms the walls of these cavities is denser than that around it, and

Fig. 198.*

Fig. 199.†

* Fig. 198. Right bony labyrinth, viewed from the outer side (after Sömmerring). $\frac{2\frac{1}{2}}{1}$.—The specimen here represented is prepared by separating piecemeal the looser substance of the petrous bone from the dense walls which immediately enclose the labyrinth. 1, the vestibule; 2, fenestra ovalis; 3, superior semicircular canal; 4, horizontal or external canal; 5, posterior canal; *, ampullæ of the semicircular canals; 6, first turn of the cochlea; 7, second turn; 8, apex; 9, fenestra rotunda. The smaller figure in outline below shows the natural size.

† Fig. 199. View of the interior of the left labyrinth (from Sömmerring). $\frac{2\frac{1}{2}}{1}$.—The bony wall of the labyrinth is removed superiorly and externally. 1, fovea hemielliptica; 2, fovea hemispherica; 3, common opening of the superior and posterior semicircular canals; 4, opening of the aqueduct of the vestibule; 5, the superior, 6, the posterior, and 7, the external semicircular canals; 8, spiral tube of the cochlea (scala tympani); 9, opening of the aqueduct of the cochlea; 10, placed on the lamina spiralis in the scala vestibuli.

forms the *osseous labyrinth;* the n
cavities forms the *membranous labyrin*
labyrinth contains a fluid called *endo*
it, between it and the osseous labyri
perilymph (see p. 678).

The osseous labyrinth consists of
namely, *the vestibule*, the *cochlea*, and
The vestibule is the middle cavity of
central organ of the whole auditory a
in its inner wall, several openings f
divisions of the auditory nerve; in its
ovalis (2, fig. 198), an opening filled b
one of the small bones of the ear;
superior walls, five openings by v
canals communicate with it: in its a
ing leading into the *cochlea*. The h
wall of the vestibule also presents a
of the *aquæductus vestibuli*, a canal l
margin of the petrous bone, with u
unknown purpose.

The *semicircular canals* (figs. 198,
cylindriform bony canals, set in the s
bone. They all open at both ends in
them first coalescing). The ends o
before opening into the vestibule; an
more dilated than the other is called
the canals form nearly vertical arche
is also anterior; the posterior is inf
is horizontal, and lower and shorter

The *cochlea* (6, 7, 8, fig. 198, a
organ, shaped like a common sn
front of the vestibule, its base r
of the internal meatus, where some
it the cochlear filaments of the a
axis, the cochlea is traversed by a
modiolus, around which a *spiral cana*

turns and a half from the base to the apex. At the apex of the cochlea the canal is closed; at the base it presents three openings, of which one, already mentioned, communicates with the vestibule; another, called *fenestra rotunda,* is separated by a membrane from the cavity of the tympanum; the third is the orifice of the *aquæductus cochleæ,* a canal leading to the jugular fossa of the petrous bone, and corresponding, at least in obscurity of purpose and origin, to the aquæductus vestibuli. The spiral canal is divided into two passages, or scalæ by a partition of bone and membrane, the *lamina spiralis.* The osseous part or *zone* of this lamina is connected with the modiolus; the membranous part, with a muscular zone, according to Todd and Bowman, forming its outer margin, is attached to the outer wall of the canal. Commencing at the base of the cochlea, between its vestibular and tympanic openings, they form a partition between these apertures; the two scalæ are, therefore, in correspondence with this arrangement, named *scala vestibuli* and *scala tympani.* At the apex of the cochlea, the lamina spiralis ends in a small *hamulus,* the inner and concave part of which, being detached from the summit of the modiolus, leaves a small aperture named *helicotrema,* by which the two scalæ, separated in all the rest of their length, communicate.

Fig. 200.*

Besides the *scala vestibuli* and *scala tympani,* there is a third space between them, in the substance of the lamina spiralis, called the *scala media,* or *canalis membranacea,* and in this are

* Fig. 200. View of the osseous cochlea divided through the middle (from Arnold). ⅝.—1, central canal of the modiolus; 2, lamina spiralis ossea; 3, scala tympani; 4, scala vestibuli; 5, porous substance of the modiolus near one of the sections of the canalis spiralis modioli.

some peculiar club-shaped little bodies called the *rods of Corti*, set up on end, with their big extremities upwards, and leaning against each other at the top—a section, therefore, having the appearance of the gable-end of a house. On their outer part are numerous cells of various shapes. The regularity with which the little rods of Corti are arranged has caused them to be compared to rows of keys in a piano.

In close relation with these rods and the cells outside them, and probably projecting also by free ends into the little triangular canal containing fluid which is between the rods, are filaments of the auditory nerve.

The *membranous labyrinth* corresponds generally with the form of the osseous labyrinth, so far as regards the vestibule and semicircular canals, but is separated from the walls of these parts by fluid, except where the nerves enter into connection within it. In the cochlea, the membranous labyrinth completes the septum between the two *scalæ*, and encloses a separate spiral canal, the *canalis membranacea*. As already mentioned, the membranous labyrinth contains a fluid called *endolymph;* and between its outer surface and the inner surface of the walls of the vestibule and semicircular canals is another collection of similar fluid, called *perilymph:* so that all the sonorous vibrations impressing the auditory nerves on these parts of the internal ear are conducted through fluid to a membrane suspended in and containing fluid. The fluid in the *scalæ* of the cochlea is continuous with the perilymph in the vestibule and semicircular canals, and there is no fluid external to its lining membrane.

The vestibular portion of the membranous labyrinth comprises two, probably communicating cavities, of which the larger and upper is named the *utriculus;* the lower, the *sacculus*. Into the former open the orifices of the membranous semicircular canals; into the latter the *canalis membranacea* of the cochlea. The membranous labyrinth of all these parts is laminated, transparent, very vascular,

and covered on the inner surface with nucleated cells, of which those that line the ampullæ are prolonged into stiff hair-like processes; the same appearance, but to a much less degree, being visible in the *utricle* and *saccule*. In the cavities of the utriculus and sacculus are small masses of calcareous particles, *otoconia* or *otolithes;* and the same, although in more minute quantities, are to be found in the interior of other parts of the membranous labyrinth.

The *auditory nerve,* for the appropriate exposure of whose filaments to sonorous vibrations all the organs now described are provided, is characterised as a nerve of special sense by its softness (whence it derived its name of *portio mollis* of the seventh pair), and by the fineness of its component fibres. It enters the labyrinth of the ear in two divisions; one for the vestibule and semicircular canals, and the other for the cochlea. The branches for the vestibule spread out and radiate on the inner surface of the membranous labyrinth: their exact determination is unknown. Those for the semicircular canals pass into the ampullæ, and form, within each of them, a forked projection which corresponds with a septum in the interior of the ampulla. The branches for the cochlea enter it through orifices at the base of the modiolus, which they ascend, and thence successively pass into canals in the osseous part of the lamina spiralis. In the canals of this osseous part or zone, the nerves are arranged in a plexus, containing ganglion cells. Their ultimate termination is not known with certainty; but some of them, without doubt, end in the organ of Corti, probably in cells.

Physiology of Hearing.

The acoustic portion of the physiology of hearing is thus illustrated by Müller: chiefly in applications of the results of his experiments on the conduction of sonorous vibrations through various combinations of air, water, and solid substances, especially membrane.

All the acoustic contrivances of the organ of hearing are means for conducting the sound, just as the optical apparatus of the eye are media for conducting the light. Since all matter is capable of propagating sonorous vibrations, the simplest conditions must be sufficient for mere hearing; for all substances surrounding the auditory nerve would communicate sound to it. In the eye a certain construction was required for directing the rays or undulations of light in such a manner that they should fall upon the optic nerve with the same relative disposition as that with which they issued from the object. In the sense of hearing this is not requisite. Sonorous vibrations, having the most various direction and the most unequal rate of succession, are transmitted by all media without modification, however manifold their decussations; and, wherever these vibrations or undulations fall upon the organ of hearing and the auditory nerves, they must cause the sensation of corresponding sounds. The whole development of the organ of hearing, therefore, can have for its object merely the *rendering more perfect* the propagation of the sonorous vibrations, and their *multiplication* by resonance; and, in fact, all the acoustic apparatus of the organ may be shown to have reference to these two principles.

Functions of the External Ear.

The external auditory passage influences the propagation of sound to the tympanum in three ways:—1, by causing the sonorous undulations, entering directly from the atmosphere, to be transmitted by the air in the passage immediately to the membrana tympani, and thus preventing them from being dispersed; 2, by the walls of the passage conducting the sonorous undulations imparted to the external ear itself, by the shortest path to the attachment of the membrana tympani, and so to this membrane; 3, by the resonance of the column of air contained within the passage.

As a conductor of undulations of air, the external auditory passage receives the direct undulations of the atmosphere, of which those that enter in the direction of its axis produce the strongest impressions. The undulations which enter the passage obliquely are reflected by its parietes, and thus by reflexion reach the membrana tympani. By reflexion, also, the external meatus receives the undulations which impinge upon the concha of the external ear, when their angle of reflexion is such that they are thrown towards the tragus. Other sonorous undulations, again, which could not enter the meatus from the external air either directly or by reflexion, may still be brought into it by inflexion; undulations, for instance, whose direction is that of the long axis of the head, and which pass over the surface of the ear, must, in accordance with the laws of inflexion, be bent into the external meatus by its margins. But the action of those undulations which enter the meatus directly are most intense; and hence we are enabled to judge of the point whence sound comes, by turning one ear in different directions, till it is directed to the point whence the vibrations may pass directly into the meatus, and produce the strongest impressions.

The walls of the meatus are also solid conductors of sound; for those vibrations which are communicated to the cartilage of the external ear, and not reflected from it, are propagated by the shortest path through the parietes of the passage to the membrana tympani. Hence, both ears, being close stopped, the sound of a pipe is heard more distinctly when its lower extremity, covered with a membrane, is applied to the cartilage of the external ear itself, than when it is placed in contact with the surface of the head.

Lastly, the external auditory passage is important, inasmuch as the air which it contains, like all insulated masses of air, increases the intensity of sounds by resonance. To convince ourselves of this, we need only lengthen the passage by affixing to it another tube: every sound that is

heard, even the sound of our own voice, is then much increased in intensity.

The action of the cartilage of the external ear upon sonorous vibrations is partly to reflect them, and partly to condense and conduct them to the parietes of the external passage. With respect to its reflecting action, the concha is the most important part, since it directs the reflected undulations towards the tragus, whence they are reflected into the auditory passage. The other inequalities of the external ear do not promote hearing by reflexion; and, if the conducting power of the cartilage of the ear were left out of consideration, they might be regarded as destined for no particular use; but receiving the impulses of the air, the cartilage of the external ear, while it reflects a part of them, propagates within itself and condenses the rest, as all other solid and elastic bodies would do. Thus, the sonorous vibrations which it receives by an extended surface, are conducted by it to its place of attachment. In consequence of the connection of the parietes of the auditory passage with the solid parts of the whole head, some dispersion of the undulations will result; but the points of attachment of the membrana tympani will receive them by the shortest path, and will as certainly communicate them to that membrane, as the solid sides of a drum communicate sonorous undulations to the parchment head, or the bridge of a musical string, its vibrations to the string.

Regarding the cartilage of the external ear, therefore, as a conductor of sonorous vibrations, all its inequalities, elevations, and depressions, which are useless with regard to reflexion, become of evident importance; for those elevations and depressions upon which the undulations fall perpendicularly, will be affected by them in the most intense degree; and, in consequence of the various form and position of these inequalities, sonorous undulations, in whatever direction they may come, must fall perpen-

dicularly upon the tangent of some one of them. This affords an explanation of the extraordinary form given to this part.

Functions of the Middle Ear: the Tympanum, Ossicula, and Fenestræ.

In animals living in the atmosphere, the sonorous vibrations are conveyed to the auditory nerve by three different media in succession; namely, the air, the solid parts of the body of the animal and of the auditory apparatus, and the fluid of the labyrinth.

Sonorous vibrations are imparted too imperfectly from air to solid bodies, for the propagation of sound to the internal ear to be adequately effected by that means alone; yet already an instance of its being thus propagated has been mentioned.

In passing from air directly into water, sonorous vibrations suffer also a considerable diminution of their strength; but if a tense membrane exists between the air and the water, the sonorous vibrations are communicated from the former to the latter medium with very great intensity. This fact, of which Müller gives experimental proof, furnishes at once an explanation of the use of the fenestra rotunda, and of the membrane closing it. They are the means of communicating, in full intensity, the vibrations of the air in the tympanum to the fluid of the labyrinth. This peculiar property of membranes is the result, not of their tenuity alone, but of the elasticity and capability of displacement of their particles; and it is not impaired when, like the membrane of the fenestra rotunda, they are not impregnated with moisture.

Sonorous vibrations are also communicated without any perceptible loss of intensity from the air to the water, when to the membrane forming the medium of communication, there is attached a short, solid body, which occupies the greater part of its surface, and is alone in contact

with the water. This fact elucidates the action of the fenestra ovalis, and of the plate of the stapes which occupies it, and, with the preceding fact, shows that both fenestræ—that closed by membrane only, and that with which the moveable stapes is connected—transmit very freely the sonorous vibrations from the air to the fluid of the labyrinth.

A small, solid body, fixed in an opening by means of a border of membrane, so as to be moveable, communicates sonorous vibrations from air on the one side, to water, or the fluid of the labyrinth, on the other side, much better than solid media not so constructed. But the propagation of sound to the fluid is rendered much more perfect if the solid conductor thus occupying the opening, or fenestra ovalis, is by its other end fixed to the middle of a tense membrane, which has atmospheric air on both sides.

A tense membrane is a much better conductor of the vibrations of air than any other solid body bounded by definite surfaces: and the vibrations are also communicated very readily by tense membranes to solid bodies in contact with them. Thus, then, the membrana tympani serves for the transmission of sound from the air to the chain of auditory bones. Stretched tightly in its osseous ring, it vibrates with the air in the auditory passage, as any thin tense membrane will when the air near it is thrown into vibrations by the sounding of a tuning-fork or a musical string. And, from such a tense vibrating membrane, the vibrations are communicated with great intensity to solid bodies which touch it at any point. If, for example, one end of a flat piece of wood be applied to the membrane of a drum while the other end is held in the hand, vibrations are felt distinctly when the vibrating tuning-fork is held over the membrane without touching it; but the wood alone, isolated from the membrane, will only very feebly propagate the vibrations of the air to the hand.

The ossicula of the ear, which are represented in this experiment by a piece of wood, are the better conductors of the sonorous vibrations communicated to them, on account of being isolated by an atmosphere of air, and not continuous with the bones of the cranium; for every solid body thus isolated by a different medium propagates vibrations with more intensity through its own substance than it communicates them to the surrounding medium, which thus prevents a dispersion of the sound; just as the vibrations of the air in the tubes used for conducting the voice from one apartment to another are prevented from being dispersed by the solid walls of the tube. The vibrations of the membrana tympani are transmitted, therefore, by the chain of ossicula to the fenestra ovalis and fluid of the labyrinth, their dispersion in the tympanum being prevented by the difficulty of the transition of vibrations from solid to gaseous bodies. The membrana tympani being a tense, solid body, bounded by free surfaces, the sonorous undulations will be partially reflected at its surfaces, so as to cause a meeting of undulations from opposite directions within it; it will, therefore, by resonance, increase the intensity of the vibrations communicated to it, and the undulations, thus rendered more intense, will act, in their turn, upon the chain of auditory bones.

The necessity of the presence of air on the inner side of the membrana tympani, in order to enable it and the ossicula auditus to fulfil the objects just described, is obvious. Without this provision, neither would the vibrations of the membrane be free, nor the chain of bones isolated, so as to propagate the sonorous undulations with concentration of their intensity. But while the oscillations of the membrana tympani are readily communicated to the air in the cavity of the tympanum, those of the solid ossicula will not be conducted away by the air, but will be propagated to the labyrinth without being dispersed

in the tympanum. Equally necessary is the communication of the air in the tympanum with the external air, through the medium of the Eustachian tube, for the maintenance of the equilibrium of pressure and temperature between them.

The propagation of sound through the ossicula of the tympanum to the labyrinth must be effected either by oscillations of the bones, or by a kind of molecular vibration of their particles, or, most probably, by both these kinds of motion.*

The long processof the malleus receives the undulations of the membrana tympani (fig. 201, *a*, *a*) and of the air in a direction indicated by the arrows, nearly perpendicular to itself. From the long process of the malleus they are propagated to its head (*b*); thence into the incus (*c*), the long process of which is parallel with the long process of the malleus. From the long process of the incus the undulations are communicated to the stapes (*d*), which is united to the incus at right angles. The several changes in the direction of the chain of bones have, however, no influence on that of the undulations, which remains the same as it was in the meatus externus and long process of the malleus, so that the undulations are communicated by the stapes to the fenestra ovalis in a perpendicular direction.

Fig. 201.

* Edouard Weber has shown that the existence of the membrane over the fenestra rotunda will permit approximation and removal of the stapes to and from the labyrinth. When by the stapes the membrane of the fenestra ovalis is pressed towards the labyrinth, the membrane of the fenestra rotunda may, by the pressure communicated through the fluid of the labyrinth, be pressed towards the cavity of the tympanum.

Increasing tension of the membrana tympani diminishes the facility of transition of sonorous undulations from the air to it. Mr. Savart observed that the dry membrana tympani, on the approach of a body emitting a loud sound, rejected particles of sand strewn upon it more strongly when lax than when very tense; and inferred, therefore, that hearing is rendered less acute by increasing the tension of the membrana tympani. Müller has confirmed this by experiments with small membranes arranged so as to imitate the membrana tympani; and it may be confirmed also by observations on one's self. For the membrana tympani on one's own person may be rendered tense at will in two ways, namely, by a strong and continued effort of expiration or of inspiration while the mouth and nostrils are closed. In the first case, the compressed air is forced with a whizzing sound into the tympanum, the membrana tympani is made tense, and immediately hearing becomes indistinct. The same temporary imperfection of hearing is produced by rendering the membrana tympani tense, and convex towards the interior, by the effort of inspiration. The imperfection of hearing, produced by the last-mentioned method, may continue for a time even after the mouth is opened, in consequence of the previous effort at inspiration having induced collapse of the walls of the Eustachian tube, which prevents the restoration of equilibrium of pressure between the air within the tympanum and that without: hence we have the opportunity of observing that even our own voice is heard with less intensity when the tension of the membrana tympani is great.

If the pressure of the external air or atmosphere be very great, while on account of collapse of the walls of the Eustachian tube, the air in the interior of the tympanum fails to exert an equal counter-pressure, the membrana tympani will of course be forced inwards, and imperfect deafness be produced. Thus it may be explained

why, in a diving-bell, voices sound
the effect of the increased tension o
pani is not to render both grave and
fainter than before. On the contra
Wollaston, the increased tension of t
produced by exhausting the cavity of
one deaf to grave sounds only.

The principal office of the Eusta
opinion, has relation to the prevent
increased tension of the membrana t
and openness will provide for th
equilibrium between the air withi
the external air, so as to prevent
of the membrana tympani which w
too great or too little pressure on eit
charging this office, however, it will
clearer, as (Henle suggests) the aper
supply the tympanum with air; an
mucus: and the ill effects of its
referred to the hindrance of all thes
of that one ascribed to it as its princ

The influence of the tensor tympa
hearing may also be probably ex
with the regulation of the tension o
pani. If, through reflex nervous a
to contraction by a very loud sound
orbicularis palpebrarum muscle ar
light, then it is manifest that a ver
through the action of this muscle, i
muffling of the ears. In favour o
have the fact that a loud sound
nervous action, winking of the eyeli
irritable nervous system, a sudden
muscles.

The influence of the stapedius
unknown. It acts upon the stapes i

make it rest obliquely in the fenestra ovalis, depressing that side of it on which it acts, and elevating the other side to the same extent.

When the fenestra ovalis and fenestra rotunda exist together with a tympanum, the sound is transmitted to the fluid of the internal ear in two ways,—namely, by solid bodies and by membrane; by both of which conducting media sonorous vibrations are communicated to water with considerable intensity. The sound being conducted to the labyrinth by two paths, will, of course, produce so much the stronger impression; for undulations will be thus excited in the fluid of the labyrinth from two different though contiguous points; and by the crossing of these undulations stationary waves of increased intensity will be produced in the fluid. Müller's experiments show that the same vibrations of the air act upon the fluid of the labyrinth with much greater intensity through the medium of the chain of auditory bones and the fenestra ovalis than through the medium of the air of the tympanum and the membrane closing the fenestra rotunda: but the cases of disease in which the ossicula have been lost without loss of hearing, prove that sound may also be well conducted through the air of the tympanum and the membrane of the fenestra rotunda.

Functions of the Labyrinth.

The fluid of the labyrinth is the most general and constant of the acoustic provisions of the labyrinth. In all forms of organs of hearing, the sonorous vibrations affect the auditory nerve through the medium of liquid—the most convenient medium, on many accounts, for such a purpose.

The function usually ascribed to the *semicircular canals* is the collecting in their fluid contents, the sonorous undulations from the bones of the cranium. They have probably,

also, in some degree, the power
the direction of their curved cavit
sounds are carried off by the su
the original direction of the undu
ducting power is in them much les
containing air.

Admitting that they have thes
intensity of the sonorous vibratio
of advantage in acting on the au
expanded in the ampullæ of the
culus. Where the membranous c
the solid parietes of the tubes, t
more intense. But the membran
must have a function independent
parts; for in the Petromyzon t
enclosed in solid substance, but
with the utriculus.

The *crystalline pulverulent masse*
re-inforce the sonorous vibrations
if they did not actually touch the
the nerves are expanded; but, in
lie in contact with the membranou
and the vestibular nerve-fibres are
communicate to these membranes
impulses of greater intensity than
can impart. This appears to be t
Sonorous undulations in water a
hand itself immersed in the wat
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hair-like prolongations from the
ampullæ have, probably, the same

The *cochlea* seems to be constru
of the nerve fibres over a wide e
solid lamina which communicates
the labyrinth and cranium, at the
contact with the fluid of the laby

exposing the nerve-fibres to the influence of sonorous undulations by two media, is itself insulated by fluid on either side.

The connection of the lamina spiralis with the solid walls of the labyrinth, adapts the cochlea for the perception of the sonorous undulations propagated by the solid parts of the head and the walls of the labyrinth. The membranous labyrinth of the vestibule and semicircular canals is suspended free in the perilymph, and is destined more particularly for the perception of sounds through the medium of that fluid, whether the sonorous undulations be imparted to the fluid through the fenestræ, or by the intervention of the cranial bones, as when sounding bodies are brought into communication with the head or teeth. The spiral lamina on which the nervous fibres are expanded in the cochlea, is, on the contrary, continuous with the solid walls of the labyrinth, and receives directly from them the impulses which they transmit. This is an important advantage; for the impulses imparted by solid bodies, have, *cæteris paribus*, a greater absolute intensity than those communicated by water. And, even when a sound is excited in the water, the sonorous undulations are more intense in the water near the surface of the vessel containing it, than in other parts of the water equally distant from the point of origin of the sound: thus we may conclude that, *cæteris paribus*, the sonorous undulations of solid bodies act with greater intensity than those of water. Hence we perceive at once an important use of the cochlea.

This is not, however, the sole office of the cochlea; the spiral lamina, as well as the membranous labyrinth, receives sonorous impulses through the medium of the fluid of the labyrinth from the cavity of the vestibule, and from the fenestra rotunda. The lamina spiralis is, indeed, much better calculated to render the action of these undulations upon the auditory nerve efficient, than the mem-

branous labyrinth is; for, as a solid body insulated by a different medium, it is capable of resonance.

The *rods of Corti* are probably arranged so that each is set to vibrate in unison with a particular tone, and thus strike a particular note, the sensation of which is carried to the brain by those filaments of the auditory nerve with which the little vibrating rod is connected.

The distinctive function therefore of these minute bodies is, probably, to render sensible to the brain the various musical notes and tones, one of them answering to one tone, and one to another; while perhaps the other parts of the organ of hearing discriminate between the intensities of different sounds, rather than their qualities.

Sensibility of the Auditory Nerve.

Most frequently, several undulations or impulses on the auditory nerve concur in the production of the impressions of sound.

By the rapid succession of several impulses at unequal intervals, a noise or rattle is produced; from a rapid succession of several impulses at equal intervals, a musical sound results, the height or acuteness of which increases with the number of the impulses communicated to the ear within a given time. A sound of definite musical value is also produced when each one of the impulses, succeeding another thus at regular intervals, is itself compounded of several undulations, in such a way that, heard alone, it would give the impression of an unmusical sound; that is to say, by a sufficiently rapid succession of short unmusical sounds at regular intervals, a musical sound is generated.

It would appear that two impulses, which are equivalent to four single or half vibrations, are sufficient to produce a definite note, audible as such through the auditory nerve. The note produced by the shocks of the teeth of a revolving wheel, at regular intervals upon a solid body, is still heard when the teeth of the wheel are removed in succession,

until two only are left; the sound produced by the impulse of these two teeth has still the same definite value in the scale of music.

The maximum and minimum of the intervals of successive impulses still appreciable through the auditory nerve as determinate sounds, have been determined by M. Savart. If their intensity is sufficiently great, sounds are still audible which result from the succession of 48,000 half vibrations, or 24,000 impulses in a second; and this, probably, is not the extreme limit in acuteness of sounds perceptible by the ear. For the opposite extreme, he has succeeded in rendering sounds audible which were produced by only fourteen or eighteen half vibrations, or seven or eight impulses in a second; and sounds still deeper might probably be heard, if the individual impulses could be sufficiently prolonged.

By removing one or several teeth from the toothed wheel before mentioned, M. Savart was also enabled to satisfy himself of the fact that in the case of the auditory nerve, as in that of the optic nerve, the sensation continues longer than the impression which causes it; for the removal of a tooth from the wheel produced no interruption of the sound. The gradual cessation of the sensation of sound renders it difficult, however, to determine its exact duration beyond that of the impression of the sonorous impulses.

The power of perceiving the *direction of sounds* is not a faculty of the sense of hearing itself, but is an act of the mind judging on experience previously acquired. From the modifications which the sensation of sound undergoes according to the direction in which the sound reaches us, the mind infers the position of the sounding body. The only true guide for this inference is the more intense action of the sound upon one than upon the other ear. But even here there is room for much deception, by the influence of reflexion or resonance, and by the propagation of sound from a distance, without loss of intensity, through

curved conducting-tubes filled with air. By means of such tubes, or of solid conductors, which convey the sonorous vibrations from their source to a distant resonant body, sounds may be made to appear to originate in a new situation.

The direction of sound may also be judged of by means of one ear only; the position of the ear and head being varied, so that the sonorous undulations at one moment fall upon the ear in a perpendicular direction, at another moment obliquely. But when neither of these circumstances can guide us in distinguishing the direction of sound, as when it falls equally upon both ears, its source being, for example, either directly in front or behind us, it becomes impossible to determine whence the sound comes.

Ventriloquists take advantage of the difficulty with which the direction of sound is recognised, and also the influence of the imagination over our judgment, when they direct their voice in a certain direction, and at the same time pretend themselves to hear the sounds as coming from thence.

The *distance of the source of sounds* is not recognised by the sense itself, but is inferred from their intensity. The sound itself is always seated but in one place, namely, in our ear; but it is interpreted as coming from an exterior soniferous body. When the intensity of the voice is modified in imitation of the effect of distance, it excites the idea of its originating at a distance; and this is also taken advantage of by ventriloquists.

The experiments of Savart, already referred to, prove that the effect of the action of sonorous undulations upon the nerve of hearing, endures somewhat longer than the period during which the undulations are passing through the ear. If, however, the impression of the same sound be very long continued, or constantly repeated for a long time, then the sensation produced may continue for a very long time, more than twelve or twenty-four hours even, after the original cause of the sound has ceased. This

must have been experienced by every one who has travelled several days continuously; for some time after the journey, the rattling noises are heard when the ear is not acted on by other sounds.

We have here a proof that the perception of sound, as sound, is not essentially connected with the existence of undulatory pulses; and that the sensation of sound is a state of the auditory nerve, which, though it may be excited by a succession of impulses, may also be produced by other causes. Even if it be supposed that undulations excited by the impulse are kept up in the auditory nerve for a certain time, they must be undulations of the nervous principle itself, which, being excited, continue until the equilibrium is restored.

Corresponding to the double vision of the same object with the two eyes, is the double hearing with the two ears; and analogous to the double vision with one eye, dependent on unequal refraction, is the double hearing of a single sound with one ear, owing to the sound coming to the ear through media of unequal conducting power. The first kind of double hearing is very rare; instances of it are recorded, however, by Sauvages and Itard. The second kind, which depends on the unequal conducting power of two media through which the same sound is transmitted to the ear, may easily be experienced. If a small bell be sounded in water, while the ears are closed by plugs, and a solid conductor be interposed between the water and the ear, two sounds will be heard differing in tensity and tone; one being conveyed to the ear through the medium of the atmosphere, the other through the conducting-rod.

The sense of vision may vary in its degree of perfection as regards either the faculty of adjustment to different distances, the power of distinguishing accurately the particles of the retina affected, sensibility to light and darkness, or the perception of the different shades of colour. In the sense of hearing, there is no parallel to the faculty

by which the eye is accommodated to distance, nor to the perception of the particular part of the nerve affected; but just as one person sees distinctly only in a bright light, and another only in a moderate light, so in different individuals the sense of hearing is more perfect for sounds of different pitch; and just as a person whose vision for the forms of objects, etc., is acute, nevertheless distinguishes colours with difficulty, and has no perception of the harmony and disharmony of colours, so one, whose hearing is good as far as regards the sensibility to feeble sounds, is sometimes deficient in the power of recognising the musical relation of sounds, and in the sense of harmony and discord; while another individual, whose hearing is in other respects imperfect, has these endowments. The causes of these differences are unknown.

Subjective sounds are the result of a state of irritation or excitement of the auditory nerve produced by other causes than sonorous impulses. A state of excitement of this nerve, however induced, gives rise to the sensation of sound. Hence the ringing and buzzing in the ears heard by persons of irritable and exhausted nervous system, and by patients with cerebral disease, or disease of the auditory nerve itself; hence also the noise in the ears heard for some time after a long journey in a rattling noisy vehicle. Ritter found that electricity also excites a sound in the ears. From the above truly subjective sound we must distinguish those dependent, not on a state of the auditory nerve itself merely, but on sonorous vibrations excited in the auditory apparatus. Such are the buzzing sounds attendant on vascular congestion of the head and ear, or on aneurismal dilatation of the vessels. Frequently even the simple pulsatory circulation of the blood in the ear is heard. To the sounds of this class belong also the snapping sound in the ear produced by a voluntary effort, and the buzz or hum heard during the contraction of the palatine muscles in the act of yawning; during the forcing

of air into the tympanum, so as to make tense the membrana tympani; and in the act of blowing the nose, as well as during the forcible depression of the lower jaw.

Irritation or excitement of the auditory nerve is capable of giving rise to movements in the body, and to sensations in other organs of sense. In both cases it is probable that the laws of reflex action, through the medium of the brain, come into play. An intense and sudden noise excites, in every person, closure of the eyelids, and, in nervous individuals, a start of the whole body or an unpleasant sensation, like that produced by an electric shock, throughout the body, and sometimes a particular feeling in the external ear. Various sounds cause in many people a disagreeable feeling in the teeth, or a sensation of cold tickling through the body, and, in some people, intense sounds are said to make the saliva collect.

The sense of hearing may in its turn be affected by impressions on many other parts of the body; especially in diseases of the abdominal viscera, and in febrile affections. Here, also, it is probable that the central organs of the nervous system are the media through which the impression is transmitted.

SENSE OF TASTE.

The conditions for the perception of taste are:—1, the presence of a nerve with special endowments; 2, the excitation of the nerves by the sapid matters, which for this purpose must be in a state of solution. The nerves concerned in the production of the sense of taste have been already considered (pp. 547 and 555).

The mode of action of the substances which excite taste probably consists in the production of a change in the internal condition of the gustatory nerves; and, according to the difference of the substances, an infinite variety of changes of condition, and consequently of tastes, may be induced. It is not, however, necessary for the manifesta-

tion of taste that sapid substances in solution should be brought into contact with its nerves. For the nerves of taste, like the nerves of other special senses, may have their peculiar properties excited by various other kinds of irritation, such as electricity and mechanical impressions. Thus Henle observed that a small current of air directed upon the tongue gives rise to a cool saline taste, like that of saltpetre; and Dr. Baly has shown that a distinct sensation of taste, similar to that caused by electricity, may be produced by a smart tap applied to the papillæ of the tongue. Moreover, the mechanical irritation of the fauces and palate produces the sensation of nausea, which is probably only a modification of taste.

The matters to be tasted must either be in solution or be soluble in the moisture covering the tongue; hence insoluble substances are usually tasteless, and produce merely sensations of touch. Moreover, for the perfect action of a sapid, as of an odorous substance, it is necessary that the sentient surface should be moist. Hence, when the tongue and fauces are dry, sapid substances, even in solution, are with difficulty tasted.

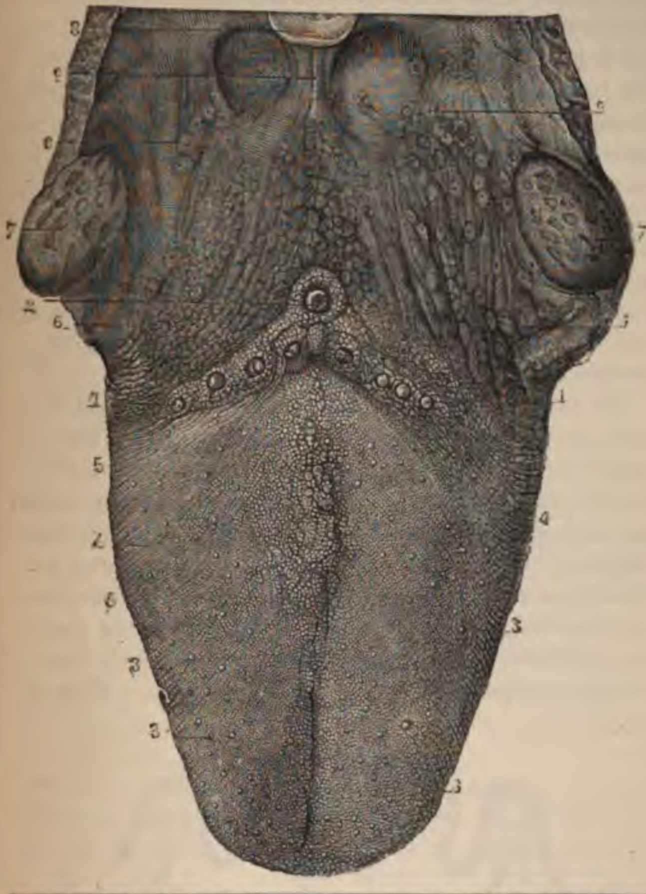
The principal, but not exclusive seat of the sense of taste is the fauces and tongue.

The tongue is a muscular organ covered by mucous membrane; the latter resembling other mucous membranes (p. 398) in essential points of structure, but containing certain parts, the *papillæ*, more or less peculiar to itself; peculiar, however, in details of structure and arrangement, not in their nature. The tongue is beset with numerous mucous follicles and glands. Its use in relation to mastication and deglutition has already been considered (p. 264).

Besides other functions, the mucous membrane of the tongue serves as a ground-work for the ramification of the abundant blood-vessels and nerves which the tongue receives, and affords insertion to the extremities of the

muscular fibres of which the chief substance of the organ is composed.

*Fig. 202.**



* Fig. 202. Papillar surface of the tongue, with the fauces and tonsils (from Sappey).—1, 1, circumvallate papillæ, in front of 2, the foramen cæcum; 3, fungiform papillæ; 4, filiform and conical papillæ; 5, transverse and oblique rugæ; 6, mucous glands at the base of the tongue and in the fauces; 7, tonsils; 8, part of the epiglottis; 9, median glosso-epiglottidean fold, frænum epiglottidis.

The larger *papillæ* of the tongue are thickly set over the anterior two-thirds of its upper surface, or *dorsum* (fig. 202), and give to it its characteristic roughness. Their greater prominence than those of the skin is due to their interspaces not being filled up with epithelium, as the interspaces of the papillæ of the skin are. The papillæ of the tongue present several diversities of form; but three principal varieties, differing both in seat and general characters, may usually be distinguished, namely, the *circumvallate* or *calyciform*, the *fungiform*, and the *filiform* papillæ. Essentially these have all of them the same structure, that is to say, they are all formed by a projection of the mucous membrane, and contain special branches of blood-vessels and nerves. In details of structure, however, they differ considerably one from another.

All the three varieties of papillæ just described have been commonly regarded as simple processes, like the papillæ of the skin; but Todd and Bowman have shown that the surface of each kind is studded by minute conical processes of mucous membrane, which thus form secondary papillæ. These secondary papillæ also occur over most other parts of the tongue, not occupied by the compound papillæ, and extend for some distance behind the papillæ circumvallatæ. The mucous membrane immediately in front of the epiglottis is, however, free from them. They are

Fig. 203.*

* Fig. 203. Vertical section of the circumvallate papillæ (from Kölliker). 10/1.—A, the papillæ; B, the surrounding wall; *a*, the epithelial covering; *b*, the nerves of the papilla and wall spreading towards the surface; *c*, the secondary papillæ.

commonly buried beneath the epithelium; hence they had been previously overlooked.

Circumvallate or Calyciform Papillæ.—These papillæ (fig. 203), eight or ten in number, are situate in two V-shaped lines at the base of the tongue (1, 1, fig. 202). They are circular elevations from $\frac{1}{20}$th to $\frac{1}{12}$th of an inch wide, each with a central depression, and surrounded by a circular fissure, at the outside of which again is a slightly elevated ring, both the central elevation and the ring being formed of close set simple papillæ (fig. 203).

*Fig. 204.**

Fungiform Papillæ.—The fungiform papillæ (fig. 204) are scattered chiefly over the sides and tip, and sparingly over the middle of the dorsum, of the tongue; their name is derived from their being usually narrower at their base than at their summit. They also consist of groups of simple papillæ, each of which contains in its interior a loop of capillary blood-vessels, and a nerve-fibre.

Conical or Filiform Papillæ.—These, which are the most abundant papillæ, are scattered over the whole surface of the tongue, but especially over the middle of the dorsum.

* Fig. 204. Surface and section of the fungiform papillæ (from Kölliker, after Todd and Bowman).—A, the surface of a fungiform papilla, partially denuded of its epithelium, $\frac{35}{1}$; *p*, secondary papillæ; *e*, epithelium. B, section of a fungiform papilla with the blood-vessels injected; *a*, artery; *v*, vein; *c*, capillary loops of simple papillæ in the neighbouring structure of the tongue; *d*, capillary loops of the secondary papillæ; *e*, epithelium.

They vary in shape somewhat, but for the most part are conical or filiform, and covered by a thick layer of epidermis, which is arranged over them, either in an imbricated manner, or is prolonged from their surface in the form of fine stiff projections, hair-like in appearance, and in some instances in structure also (fig. 205). From their peculiar structure, it seems likely that these papillæ have a mechanical function, or one allied to that of touch, rather than of taste; the latter sense being probably seated especially in the other two varieties of papillæ, the *circumvallate* and the *fungiform*.

*Fig. 205.**

The *epithelium* of the tongue is of the squamous or tesselated kind (p. 30). It covers every part of the surface; but over the fungiform papillæ

* Fig. 205. Two filiform papillæ, one with epithelium, the other without (from Kölliker, after Todd and Bowman). $\frac{30}{1}$.—*p*, the substance of the papillæ dividing at their upper extremities into secondary papillæ; *a*, artery, and *v*, vein, dividing into capillary loops; *e*, epithelial covering, laminated between the papillæ, but extended into hair-like processes *f*, from the extremities of the secondary papillæ.

forms a thinner layer than elsewhere, so that these papillæ stand out more prominently than the rest. The epithelium covering the filiform papillæ has been shown by Todd and Bowman, to have a singular arrangement; being extremely dense and thick, and, as before mentioned, projecting from their sides and summits in the form of long, stiff, hair-like processes. Many of these processes bear a close resemblance to hairs, and some actually contain minute hair-tubes. Blood-vessels and nerves are supplied freely to the papillæ. The nerves in the fungiform and circumvallate papillæ form a kind of plexus, spreading out brush-wise (fig. 203), but the exact mode of termination of the nerve filaments is not certainly known.

Such, in outline, is the structure of the sensitive surface of the tongue. But the tongue is not the only seat of the sense of taste; for the results of experiments as well as ordinary experience show that the soft palate and its arches, the uvula, tonsils, and probably the upper part of the pharynx, are endowed with taste. These parts, together with the base and posterior parts of the tongue, are supplied with branches of the glosso-pharyngeal nerve, and evidence has been already adduced (p. 556 *et seq.*) that the sense of taste is conferred upon them by this nerve.

In most, though not in all persons, the anterior part of the tongue, especially the edges and tip, are endowed with the sense of taste. The middle of the dorsum is only feebly endowed with this sense, probably because of the density and thickness of the epithelium covering the filiform papillæ of this part of the tongue, which will prevent the sapid substances from penetrating to their sensitive parts. The gustatory property of the anterior part of the tongue is due, as already said (p. 547), to the lingual branches of the fifth nerve.

Besides the sense of taste, the tongue, by means also of its papillæ, is endued, especially at its sides and tip, with

a very delicate and accurate sense of touch, which renders it sensible of the impressions of heat and cold, pain and mechanical pressure, and consequently of the form of surfaces. The tongue may lose its common sensibility, and still retain the sense of taste, and *vice versâ*. This fact renders it probable that, although the senses of taste and of touch may be exercised by the same papillæ supplied by the same nerves, yet the nervous conductors for these two different sensations are distinct, just as the nerves for smell and common sensibility in the nostrils are distinct; and it is quite conceivable that the same nervous trunk may contain fibres differing essentially in their specific properties. Facts already detailed (p. 547) seem to prove that the lingual branch of the fifth nerve is the seat of sensations of taste in the anterior part of the tongue: and it is also certain, from the marked manifestations of pain to which its division in animals gives rise, that it is likewise a nerve of common sensibility. The glosso-pharyngeal also seems to contain fibres both of common sensation and of the special sense of taste.

The concurrence of common and special sensibility in the same part makes it sometimes difficult to determine whether the impression produced by a substance is perceived through the ordinary sensitive fibres, or through those of the sense of taste. In many cases, indeed, it is probable that both sets of nerve-fibres are concerned, as when irritating acrid substances are introduced into the mouth.

The impressions on the mind leading to the perception of taste seem to result, as already said, from certain changes in the internal condition of the nerves produced by the contact of sapid substances with the papillæ in which the fibres of these nerves are distributed. This explanation, obscure though it be, may account generally for the sense; but the variations of taste produced by different substances are as yet inexplicable. In the case

of hearing, we know that sounds differ from one another according to the differences in the number of undulations producing them; and in the case of vision, it is reasonably inferred that different colours result from differences in the number of undulations, or in the rate of transit, of the principle of light. But, in the cases of taste and smell, no such probable explanation has yet been offered. It would appear, indeed, from the experiments of Horn, that while some substances taste alike in all regions of the tongue's surface, others excite different tastes, according as they are applied to different papillæ of the tongue. This observation, if confirmed, would seem to show that, in some cases at least, different fibres are capable of receiving different impressions from the same sapid substance.

Much of the perfection of the sense of taste is often due to the sapid substances being also odorous, and exciting the simultaneous action of the sense of smell. This is shown by the imperfection of the taste of such substances when their action on the olfactory nerves is prevented by closing the nostrils. Many fine wines lose much of their apparent excellence if the nostrils are held close while they are drunk.

Very distinct sensations of taste are frequently left after the substances which excited them have ceased to act on the nerve; and such sensations often endure for a long time, and modify the taste of other substances applied to the tongue afterwards. Thus, the taste of sweet substances spoils the flavour of wine, the taste of cheese improves it. There appears, therefore, to exist the same relation between tastes as between colours, of which those that are opposed or complementary render each other more vivid, though no general principles governing this relation have been discovered in the case of tastes. In the art of cooking, however, attention has at all times been paid to the consonance or harmony of flavours in their combination or order of succession, just as in painting and music the

fundamental principles of harmony have been employed empirically while the theoretical laws were unknown.

Frequent and continued repetitions of the same taste render the perception of it less and less distinct, in the same way that a colour becomes more and more dull and indistinct the longer the eye is fixed upon it. Thus, after frequently tasting first one and then the other of two kinds of wine, it becomes impossible to discriminate between them.

The simple contact of a sapid substance with the surface of the gustatory organ seldom gives rise to a distinct sensation of taste; it needs to be diffused over the surface, and brought into intimate contact with the sensitive parts by compression, friction, and motion between the tongue and palate.

The sense of taste seems capable of being excited also by internal causes, such as changes in the conditions of the nerves or nerve-centres, produced by congestion or other causes, which excite subjective sensations in the other organs of sense. But little is known of the subjective sensations of taste; for it is difficult to distinguish the phenomena from the effects of external causes, such as changes in the nature of the secretions of the mouth.

SENSE OF TOUCH.

The sense of touch is not confined to particular parts of the body of small extent, like the other senses; on the contrary, all parts capable of perceiving the presence of a stimulus by ordinary sensation are, in certain degrees, the seat of this sense; for touch is simply a modification or exaltation of common sensation or sensibility. The nerves on which the sense of touch depends are, therefore, the same as those which confer ordinary sensation on the different parts of the body, viz., those derived from the posterior roots of the nerves of the spinal cord, and the sensitive cerebral nerves.

But, although all parts of the body supplied with sensitive nerves are thus, in some degree, organs of touch, yet the sense is exercised in perfection only in those parts the sensibility of which is extremely delicate, *e.g.*, the skin, the tongue, and the lips, which are provided with abundant papillæ. (See chapter on SKIN, and section on TASTE.)

The sensations of the common sensitive nerves have as peculiar a character as those of any other organ of sense. The sense of touch renders us conscious of the presence of a stimulus, from the slightest to the most intense degree of its action, neither by sound, nor by light, nor by colour, but by that indescribable something which we call feeling, or common sensation. The modifications of this sense often depend on the extent of the parts affected. The sensation of pricking, for example, informs us that the sensitive particles are intensely affected in a small extent; the sensation of pressure indicates a slighter affection of the parts in a greater extent, and to a greater depth. It is by the depth to which the parts are affected that the feeling of pressure is distinguished from that of mere contact. Schiff and Brown-Séquard are of opinion that common sensibility and tactile sensibility manifest themselves to the individual by the aid of different sets of fibres. Dr. Sieveking has arrived at the same conclusion from pathological observation.

By the sense of touch the mind is made acquainted with the size, form, and other external characters of bodies. And in order that these characters may be easily ascertained, the sense of touch is especially developed in those parts which can be readily moved over the surface of bodies. Touch, in its more limited sense, or the act of examining a body by the touch, consists merely in a voluntary employment of this sense combined with movement, and stands in the same relation to the sense of touch, or common sensibility, generally, as the act of seek-

ing, following, or examining odours, does to the sense of smell. Every sensitive part of the body which can, by means of movement, be brought into different relations of contact with external bodies, is an organ of "touch." No one part, consequently, has exclusively this function. The hand, however, is best adapted for it, by reason of its peculiarities of structure,—namely, its capability of pronation and supination, which enables it, by the movement of rotation, to examine the whole circumference of a body; the power it possesses of opposing the thumb to the rest of the hand; and the relative mobility of the fingers. Besides—the hand, and especially the fingers, are abundantly endowed with *papillæ* and *touch-corpuscles* (pp. 424, 425) which are specially necessary for the perfect employment of this sense.

In forming a conception of the figure and extent of a surface, the mind multiplies the size of the hand or fingers used in the inquiry by the number of times which it is contained in the surface traversed; and by repeating this process with regard to the different dimensions of a solid body, acquires a notion of its cubical extent.

The perfection of the sense of touch on different parts of the surface is proportioned to the power which such parts possess of distinguishing and isolating the sensations produced by two points placed close together. This power depends, at least in part, on the number of primitive nerve-fibres distributed to the part; for the fewer the primitive fibres which an organ receives, the more likely is it that several impressions on different contiguous points will act on only one nervous fibre, and hence be confounded, and perhaps produce but one sensation. Experiments to determine the tactile properties of different parts of the skin, as measured by this power of distinguishing distances, were made by E. H. Weber. One experiment consisted in touching the skin, while the eyes were closed, with the points of a pair of compasses sheathed

with cork, and in ascertaining how close the points of the compasses might be brought to each other, and still be felt as two bodies. He examined in this manner nearly every part of the surface of the body, and has given tables showing the relative degrees of sensibility of different parts. Experiments of a similar kind have been performed also by Valentin: and, among the numerous results obtained by both these investigators, it appears that the extremity of the third finger, and the point of the tongue are the parts most sensitive: a distance of as little as half a line being here distinguished. Next in sensitiveness to these is the mucous surface of the lips, which can perceive the two points of the compass when separated to the distance of about a line and a half: on the dorsum of the tongue they require to be separated two lines. The parts in which the sense of touch is least acute are the neck, the middle of the back, the middle of the arm, and the middle of the thigh, on which the points of the compass have to be separated to the distance of thirty lines to be perceived as distinct points (Weber). Other parts of the body possess various degrees of sensibility intermediate between the above extremes.

A sensation in a part endowed with touch appears to the mind to be, *cæteris paribus*, more intense when it is excited in a large extent of surface than when it is confined to a small space. The temperature of water into which he dipped his whole hand, appeared to Weber to be higher than that of water of really higher temperature, in which he immersed only one finger of the other hand. Similar observations may be made by persons bathing in warm or cold water.

Part of the ideas which we obtain of the conditions of external bodies is derived through the peculiar sensibility with which muscles are endowed—the sensibility by which we are made acquainted with their position, and the degree of their contraction. By this sensation, we are enabled to

estimate the degree of force exerted in resisting pressure or in raising weights. The estimate of weight by muscular effort is more accurate than that by pressure on the skin, according to Weber, who states that by the former a difference between two weights may be detected when one is only one-twentieth or one-fifteenth less than the other. It is not the absolute, but the relative, amount of the difference of weight which we have thus the faculty of perceiving.

It is not, however, certain, that our idea of the amount of muscular force used is derived solely from sensation in the muscles. We have the power of estimating very accurately beforehand, and of regulating, the amount of nervous influence necessary for the production of a certain degree of movement. When we raise a vessel, with the contents of which we are not acquainted, the force we employ is determined by the idea we have conceived of its weight. If it should happen to contain some very heavy substance, as quicksilver, we shall probably let it fall; the amount of muscular action, or of nervous energy, which we had exerted, being insufficient. The same thing occurs sometimes to a person descending stairs in the dark; he makes the movement for the descent of a step which does not exist. It is possible that in the same way the idea of weight and pressure in raising bodies, or in resisting forces, may in part arise from a consciousness of the amount of nervous energy transmitted from the brain rather than from a sensation in the muscles themselves. The mental conviction of the inability longer to support a weight must also be distinguished from the actual sensation of fatigue in the muscles.

So, with regard to the ideas derived from sensation of touch combined with movements, it is doubtful how far the consciousness of the extent of muscular movement is obtained from sensations in the muscles themselves. The sensation of movement attending the motions of the hand

is very slight; and persons who do not know that the action of particular muscles is necessary for the production of given movements, do not suspect that the movement of the fingers, for example, depends on an action in the fore-arm. The mind has, nevertheless, a very definite knowledge of the changes of position produced by movements; and it is on this that the ideas which it conceives of the extension and form of a body are in great measure founded.

In order that an impression made on a sensitive surface may be perceived, it is necessary that there should exist a reciprocal influence between the mind and the sense of touch; for, if the mind does not thus co-operate, the organic conditions for the sensation may be fulfilled, but it remains unperceived. Moreover, the distinctness and intensity of a sensation in the nerves of touch depend, in great measure, on the degree in which the mind co-operates for its perception. A painful sensation becomes more intolerable the more the attention is directed to it: thus, a sensation in itself inconsiderable, as an itching in a very small spot of the skin, may be rendered very troublesome and enduring.

As every sensation is attended with an idea, and leaves behind it an idea in the mind which can be reproduced at will, we are enabled to compare the idea of a past sensation with another sensation really present. Thus we can compare the weight of one body with another which we had previously felt, of which the idea is retained in our mind. Weber was indeed able to distinguish in this manner between temperatures, experienced one after the other, better than between temperatures to which the two hands were simultaneously subjected. This power of comparing present with past sensations diminishes, however, in proportion to the time which has elapsed between them.

The *after-sensations* left by impressions on nerves of common sensibility or touch are very vivid and durable. As

long as the condition into which the stimulus has thrown the organ endures, the sensation also remains, though the exciting cause should have long ceased to act. Both painful and pleasurable sensations afford many examples of this fact.

The law of *contrast*, which we have shown modifies the sensations of vision, prevails here also. After the body has been exposed to a warm atmosphere, a degree of temperature a very little lower, which would under other circumstances appear warm, produces the sensation of cold; and a sudden change to the extent of a few degrees from a cold temperature to one less severe, will produce the sensation of warmth. Heat and cold are, therefore, relative terms; for a particular state of the sentient organs causes what would otherwise be warmth to appear cold. So, also a diminution in the intensity of a long-continued pain gives pleasure, even though the degree of pain that remains would in the healthy state have seemed intolerable.

Subjective sensations, or sensations dependent on internal causes, are in no sense more frequent than in the sense of touch. All the sensations of pleasure and pain, of heat and cold, of lightness and weight, of fatigue, etc., may be produced by internal causes. Neuralgic pains, the sensation of rigor, formication or the creeping of ants, and the states of the sexual organs occurring during sleep, afford striking examples of subjective sensations.

The mind, also, has a remarkable power of exciting sensations in the nerves of common sensibility; just as the thought of the nauseous excites sometimes the sensation of nausea, so the idea of pain gives rise to the actual sensation of pain in a part predisposed to it. The thought of anything horrid excites the sensation of shuddering; the feelings of eager expectation, of pathetic emotion, of enthusiasm, excite in some persons a sensation of "concentration" at the top of the head, and of cold trickling

through the body; fright causes sensations to be felt in many parts of the body; and even the thought of tickling excites that sensation in individuals very susceptible of it, when they are threatened with it by the movements of another person. These sensations from internal causes are most frequent in persons of excitable nervous systems, such as the hypochondriacal and the hysterical, of whom it is usual to say that their pains are imaginary. If by this is meant that their pains exist in their imagination merely, it is certainly quite incorrect. Pain is never imaginary in this sense; but is as truly pain when arising from internal as from external causes; the idea of pain only can be unattended with sensation, but of the mere idea no one will complain. Still, it is quite certain that the imagination can render pain that already exists more intense and can excite it when there is a disposition to it.

CHAPTER XX.

GENERATION AND DEVELOPMENT.

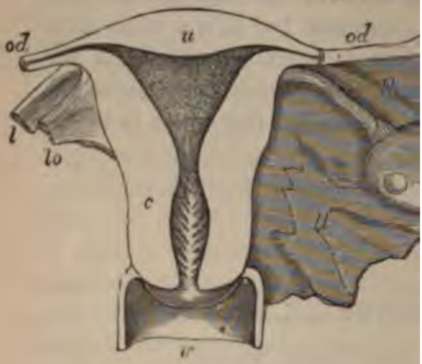
The several organs and functions of the human body which have been considered in the previous chapters, have relation to the individual being. We have now to consider those organs and functions which are destined for the propagation of the species. These comprise the several provisions made for the formation, impregnation, and development of the ovum, from which the embryo or fœtus is produced and gradually perfected into a fully-formed human being.

The organs concerned in effecting these objects are named the generative organs, or sexual apparatus, since part belong to the male and part to the female sex.

Generative Organs of

The female organs of generation
whose function is the formation
tube, or oviduct, connected with e
pose of conducting the ovum from
or cavity in which, if impregnated,
embryo is fully developed, and
existence, independently of intern
parent; and, lastly, of a canal, or
ages, for the reception of the male

Fig. 206.



* Fig. 206. Diagrammatic view of the
as seen from behind (from Quain). ½.—
of the vagina have been laid open by rem
Fallopian tube, round ligament, and ova
short, and the broad ligament removed
part of the uterus; *c*, the cervix opposite th
shape of the uterine cavity is shown, and
cavity with the rugæ termed arbor vitæ;
od, Fallopian tube or oviduct; the narrow
with that of the cornu of the uterus on
ligament; *lo*, ligament of the ovary; *o*,
the right Fallopian tube; *fi*, its fimbriate
h, one of the hydatids frequently foun
ligament.

act of copulation, and for the subsequent discharge of the fœtus.

The *ovaries* are two oval compressed bodies, situated in the cavity of the pelvis, one on each side, enclosed in the folds of the broad ligament. Each ovary is attached to the uterus by a narrow fibrous cord (the ligament of the ovary), and, more slightly, to the Fallopian tube by one of the fimbriæ, into which the walls of the extremity of the tube expand.

The ovary is enveloped by a *capsule* of dense fibro-cellular tissue, which again is surrounded by peritoneum. The internal structure of the organ consists of a peculiar soft fibrous tissue, or *stroma*, abundantly supplied with blood-vessels, and having embedded in it, in various stages of development, numerous minute follicles or vesicles, the *Graafian vesicles*, or sacculi, containing the ova (fig. 207). A further account of the Graafian vesicles and of their contained ova will be presently given.

The *Fallopian tubes* are about four inches in length, and extend between the ovaries and the upper angles of the uterus. At the point of attachment to the uterus, the Fallopian tube is very narrow; but in its course to the ovary it increases to about a line and a half in thickness; at its distal extremity, which is free and floating, it bears a number of *fimbriæ*, one of which, longer than the rest, is attached to the ovary. The canal by which each Fallopian tube is traversed is narrow, especially at its point of entrance into the uterus, at which it will scarcely admit a bristle; its other extremity is wider, and opens into the cavity of the abdomen, surrounded by the zone of fimbriæ. Externally, the Fallopian tube is invested with peritoneum; internally, its canal is lined with mucous membrane, covered with ciliary epithelium (p. 33): between the peritoneal and mucous coats, the walls are composed, like those of the uterus, of fibrous tissue and organic muscular fibres (pp. 581-3).

The *uterus* (*u*, *c*, fig. 206) is a som
organ, with a central cavity lined w
In the unimpregnated state it is
length, two in breadth at its upper p

Fig. 207.

lower pointed part or *neck*, only abo
part between the fundus and neck
the uterus: it is about an inch in
of the organ are composed of den
with which are intermingled fibres
the impregnated state the latter ar
increased in number. The cavity o

---

* Fig. 207. View of a section of the pr
Schrön) ♀.—1. outer covering and free bord
border; 2, the ovarian stroma, presenting a f
3, granular substance lying external to th
vessels; 5, ovigerms in their earliest sta
granular layer near the surface; 6, ovig
enlarge and to pass more deeply into th
which the Graafian follicle and tunica gra
which have passed somewhat deeper into th
by the fibrous stroma; 8, more advance
ovum imbedded in the layer of cells consti
9, the most advanced follicle containing
from which the ovum has accidentally esca

in form to that of the organ itself: it is very small in the unimpregnated state; the sides of its mucous surface being almost in contact, and probably only separated from each other by mucus. Into its upper part, at each side, opens the canal of the corresponding Fallopian tube: below, it communicates with the vagina by a fissure-like opening in its neck, the *os uteri*, the margins of which are distinguished into two lips, an anterior and posterior. In the mucous membrane of the cervix are found several mucous follicles, termed ovula or glandulæ Nabothi: they probably form the jelly-like substance by which the os uteri is usually found closed.

The *vagina* is a membranous canal, six or eight inches long, extending obliquely downwards and forwards from the neck of the uterus, which it embraces, to the external organs of generation. It is lined with mucous membrane, which in the ordinary contracted state of the canal, is thrown into transverse folds. External to the mucous membrane, the walls of the vagina are constructed of fibro-cellular tissue, within which, especially around the lower part of the tube, is a layer of erectile tissue. The lower extremity of the vagina is embraced by an orbicular muscle, the constrictor vaginæ; its external orifice, in the virgin, is partially closed by a fold or ring of mucous membrane, termed the *hymen*. The external organs of generation consist of the *clitoris*, a small elongated body, situated above and in the middle line, and constructed, like the male penis, of two erectile corpora cavernosa, but unlike it, without a corpus spongiosum, and not perforated by the urethra; of two folds of mucous membrane, termed *labia interna*, or *nymphæ;* and, in front of these, of two other folds, the *labia externa*, or *pudenda*, formed of the external integument, and lined internally by mucous membrane. Between the nymphæ and beneath the clitoris is an angular space, termed the vestibule, at the centre of whose base is the orifice of the meatus urinarius. Numerous

mucous follicles are scattered beneath the mucous membrane composing these parts of the external organs of generation; and at the side of the fore part of the vagina, are two larger lobulated glands, named *vulvo-vaginal*, or Duverney's glands, which are analogous to Cowper's glands in the male.

Having given this general outline of the several parts which, in the female, contribute to the reproduction of the species, it will now be necessary to examine successively the formation, discharge, impregnation, and development of the ovum, to which these several parts are subservient.

Unimpregnated Ovum.

If the *structure and formation* of the human ovary be examined at any period between early infancy and advanced age, but especially during that period of life in which the power of conception exists, it will be found to contain, on an average, from fifteen to twenty small vesicles or membranous sacs of various sizes; these have been already alluded to as the *follicles* or *vesicles* of *De Graaf*, the anatomist who first accurately described them; they are also sometimes called *ovisacs*. At their first formation, the Graafian vesicles, according to Schrön, are near the surface of the stroma of the ovary, but subsequently become more deeply placed; and again, as they increase in size, make their way towards the surface. When mature, they form little prominences on the exterior of the ovary, covered only by the peritoneum. Each follicle has an external membranous envelope, composed of fine fibro-cellular tissue, and connected with the surrounding stroma of the ovary by networks of blood-vessels (fig. 208). This envelope or tunic is lined with a layer of nucleated cells, forming a kind of epithelium or internal tunic, and named *membrana granulosa*. The cavity of the follicle is filled with an albuminous fluid in which microscopic granules float; and it contains also the *ovum* or *ovule*.

The ovum is a minute spherical body situated, in immature follicles, near the centre; but in those nearer maturity, in contact with the membrana granulosa at that part of the follicle which forms a prominence on the surface of the ovary. The cells of the membrana granulosa are at that point more numerous than elsewhere, and are heaped around the ovum, forming a kind of granular zone, the *discus proligerus* (fig. 208).

Fig. 208.*

In order to examine an ovum, one of the Graafian vesicles, it matters not whether it be of small size or arrived at maturity, should be pricked, and the contained fluid received upon a piece of glass. The ovum then, being found in the midst of the fluid by means of a simple lens, may be further examined with higher microscopic powers. Owing to its globular form, however, its structure cannot be seen until it is subjected to gentle pressure.

The human ovum is extremely small, measuring, according to Bischoff, from $\frac{1}{240}$ to $\frac{1}{220}$ of an inch. Its external investment is a transparent membrane, about $\frac{1}{2500}$ of an inch in thickness, which under the microscope, appears as a bright ring (fig. 209), bounded externally and internally by a dark outline: it is called the *zona pellucida*, or *vitelline membrane*. It adheres externally to the heap of cells constituting the discus proligerus.

Within this transparent investment or zona pellucida,

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* 208. Section of the Graafian vesicle of a Mammal, after Von Baer. 1. Stroma of the ovary with blood-vessels. 2. Peritoneum. 3 and 4. Layers of the external coat of the Graafian vesicle. 5. Membrana granulosa. 6. Fluid of the Graafian vesicle. 7. Granular zone, or discus proligerus, containing the ovum (8).

and usually in close contact with it, lies the yolk or vitellus which is composed of granules and globules of various sizes, imbedded in a more or less fluid substance. The smaller granules, which are the more numerous, resemble in their appearance, as well as their constant motion, pigment-granules. The larger granules or globules which have the aspect of fat-globules, are in greatest number at the periphery of the yelk. The number of the granules is, according to Bischoff, greatest in the ova of carnivorous animals. In the human ovum their quantity is comparatively small.

*Fig. 209.**

In the substance of the yelk is imbedded the *germinal vesicle*, or vesicula germinativa (figs. 209, 210). This vesicle is of greatest relative size in the smallest ova, and is in them surrounded closely by the yelk, nearly in the centre of which it lies. During the development of the ovum, the germinal vesicle increases in size much less rapidly than the yelk, and comes to be placed near to its surface. Its size in the human ovum has not yet been ascertained, owing to the difficulty of isolating it; but it is probably about $\frac{1}{720}$ of an inch in diameter. It consists of a fine, transparent, structureless membrane, containing a clear, watery fluid, in which are sometimes a few granules; and at that part of the periphery of the germinal vesical which is nearest to the periphery of the yelk is situated the *germinal spot* (*macula germinativa*), a finely granulated substance, of a yellowish colour, strongly refracting the rays of light, and measuring, in the Mammalia generally, from $\frac{1}{3600}$ to $\frac{1}{2400}$ of an inch (Wagner).

* Fig. 209. Ovum of the sow, after Barry. 1. Germinal spot. 2. Germinal vesicle. 3. Yelk. 4. Zona pellucida. 5. Discus proligerus. 6. Adherent granules or cells.

Such are the parts of which the Graafian follicle and its contents, including the ovum, are composed. The diagram (fig. 210) represents them in their relative positions when mature. With regard to the mode and order of development of these parts there is considerable uncertainty; but it seems most likely that the ovum is formed before the Graafian vesicle or ovisac.

Fig. 210.*

With regard to the parts of the *ovum* first formed, it appears certain that the formation of the germinal vesicle precedes that of the yelk and zona pellucida, or vitelline membrane. Whether the germinal spot is formed first, and the germinal vesicle afterwards developed around it, cannot be decided in the case of vertebrate animals; but the observations of Kölliker and Bagge on the development of the ova of intestinal worms show that in these animals, the first step in the process is the production of round bodies resembling the germinal spots of ova, the

* Fig. 210. Diagram of a Graafian vesicle, containing an ovum. 1. Stroma or tissue of the ovary. 2 and 3. External and internal tunics of the Graafian vesicle. 4. Cavity of the vesicle. 5. Thick tunic of the ovum or yelk sac. 6. The yelk. 7. The germinal vesicle. 8. The germinal spot.

germinal vesicles being subsequently developed around these in the form of transparent membranous cells.

The more important changes that take place in the ovum next to the formation of these its essential component parts, consist in alterations of the size and position of these parts with relation to each other, and of the ovum itself with relation to the Graafian vesicle, and in the more complete elaboration of the yelk. The earlier the stage of development the larger is the germinal vesicle in relation to the whole ovum, and of the ovum in relation to the Graafian vesicle. For, as the ovum becomes mature, although all these parts increase in size, the Graafian vesicle enlarges most, and the germinal vesicle least. Changes take place also in the position of the parts. The ovum at first occupies the centre of the Graafian vesicle, but subsequently is removed to its periphery. The germinal vesicle, too, which in young ova is in the centre of the yelk, is in mature ova found at the periphery.

The change of position of the ovum, from the centre to the periphery of the Graafian vesicle, is possibly connected with the formation of the membrana granulosa which lines the vesicle. For, according to Valentin, at a very early period, the contents of the vesicle between its wall and the ovum are almost wholly formed of granules; but in the process of growth a clear fluid collects in the centre of the vesicle, and the granules, which from the first have a regular arrangement, are pushed outwards, and form the membrana granulosa. Now, as the mature ovum lies embedded in a thickened portion of the membrana granulosa, it is possible that when the elementary parts of this membrane are pushed outwards, in the way just described, the ovum is carried with them from the centre to the periphery of the follicle. While the changes here described take place, the zona pellucida increases in thickness.

According to Bischoff, the number of the granules of the yelk is greater the more mature the ovum, consequently the yelk is more opaque in the mature, and more transparent in the immature ova. The matter in which the granules are contained is fluid in the immature ova of all animals; in some it remains so; but in others, as the human ovum, it subsequently becomes a consistent gelatinous substance.

From the earliest infancy, and through the whole fruitful period of life, there appears to be a constant formation, development, and maturation of Graafian vesicles, with their contained ova. Until the period of puberty, however, the process is comparatively inactive; for, previous to this period, the ovaries are small and pale, the Graafian vesicles in them are very minute, few in number, and probably never attain full development, but soon shrivel and disappear, instead of bursting, as matured follicles do; the contained ova are also incapable of being impregnated. But, coincident with the other changes which occur in the body at the time of puberty, the ovaries enlarge, and become very vascular, the formation of Graafian vesicles is more abundant, the size and degree of development attained by them are greater, and the ova are capable of being fecundated.

Discharge of the Ovum.

In the process of development of individual vesicles, it has been already observed, that as each increases in size, it gradually approaches the surface of the ovary, and when fully ripe or mature, forms a little projection on the exterior. Coincident with the increase of size, caused by the augmentation of its liquid contents, the external envelope of the distended vesicle becomes very thin and eventually bursts. By this means, the ovum and fluid contents of the Graafian

vesicle are liberated, and escape on the exterior of the ovary, whence they pass into the Fallopian tube, the fimbriated processes of the extremity of which are supposed coincidentally to grasp the ovary, while the aperture of the tube is applied to the part corresponding to the matured and bursting vesicle.

In animals whose capability of being impregnated occurs at regular periods, as in the human subject, and most Mammalia, the Graafian vesicles and their contained ova appear to arrive at maturity, and the latter to be discharged at such periods only. But in other animals, *e.g.*, the common fowl, the formation, maturation, and discharge of ova appear to take place almost constantly.

It has long been known, that in the so-called oviparous animals, the separation of ova from the ovary may take place independently of impregnation by the male, or even of sexual union. And it is now established that a like maturation and discharge of ova, independently of coition, occurs in Mammalia, the periods at which the matured ova are separated from the ovaries and received into the Fallopian tubes being indicated in the lower Mammalia, by the phenomena of *heat* or *rut;* in the human female by the phenomena of *menstruation*. Sexual desire manifests itself in the human female to a greater degree at these periods, and in the female of mammiferous animals at no other time. If the union of the sexes take place, the ovum may be fecundated, and if no union occur it perishes.

That this maturation and discharge occur periodically, and only during the phenomena of heat in the lower Mammalia, is made probable by the facts that, in all instances in which Graafian vesicles have been found presenting the appearance of recent rupture, the animals were at the time, or had recently been, in heat; that on the other hand, there is no authentic and detailed account of

Graafian vesicles being found ruptured in the intervals of the periods of heat; and that female animals do not admit the males, and never become impregnated, except at those periods.

Many circumstances make it probable that the human female is subject, in these respects, to the same law as the females of other mammiferous animals; namely, that in her as in them, ova are matured and discharged from the ovary independent of sexual union, and that this maturation and discharge occur periodically at the epochs of menstruation. Thus Graafian vesicles recently ruptured have been frequently seen in ovaries of virgins or women who could not have been recently impregnated, and although it is true that the ova discharged under these circumstances have rarely been discovered in the Fallopian tube,* partly on account of their minute size, and partly because the search has seldom been prosecuted with much care, yet analogy forbids us to doubt that in the human female, as in the domestic quadrupeds, the result and purpose of the rupture of the follicles is the discharge of the ova.

The evidence of the periodical discharge of ova at the epochs of menstruation is first, that nearly all authors who have touched on the point, agree that no traces of follicles having burst are ever seen in the ovaries before puberty or the first menstruation; secondly, that in all cases in which ovarian follicles have been found burst, independently of sexual intercourse, the women were at the time menstruating, or had very recently passed through the menstrual state; thirdly, that although conception is not confined to the periods of menstruation, yet it is more likely to occur within a few days after the cessation of the

* See, however, the record of two such cases by Dr. Letheby, in the Philosophical Transactions, 1851.

menstrual flux than at other times; and, lastly, that the ovaries of the human female become turgid and vascular at the menstrual periods, as those of animals do at the time of heat.

From what has been said, it may, therefore, be concluded that the two states, heat and menstruation, are analogous, and that the essential accompaniment of both, is the maturation and extrusion of ova. In both there is a state of active congestion of the sexual organs, sympathising with the ovaries at the time of the highest degree of development of the Graafian vesicles; and in both, the crisis of this state of congestion is attended by a discharge of blood or mucus, or both, from the external organs of generation.

The occurrence of a menstrual discharge is one of the most prominent indications of the commencement of puberty in the female sex; though its absence even for several years is not necessarily attended with arrest of the other characters of this period of life, or with inaptness for sexual union, or incapability of impregnation. The average time of its first appearance in females of this country and others of about the same latitude, is from fourteen to fifteen; but it is much influenced by the kind of life to which girls are subjected, being accelerated by habits of luxury and indolence, and retarded by contrary conditions. On the whole, its appearance is earlier in persons dwelling in warm climes than in those inhabiting colder latitudes; though the extensive investigations of Mr. Roberton show that the influence of temperature on the development of puberty has been exaggerated. Much of the influence attributed to climate appears due to the custom prevalent in many hot countries, as in Hindostan, of giving girls in marriage at a very early age, and inducing sexual excitement previous to the proper menstrual time. The menstrual functions continue through the

whole fruitful period of a woman's life, and usually cease between the forty-fifth and fiftieth years.

The several menstrual periods usually occur at intervals of a lunar month, the duration of each being from three to six days. In some women the intervals are as short as three weeks or even less; while in others they are longer than a month. The periodical return is usually attended by pain in the loins, a sense of fatigue in the lower limbs, and other symptoms, which are different in different individuals. Menstruation does not usually occur in pregnant women, or in those who are suckling; but instances of its occurrence in both these conditions are by no means rare.

The menstrual discharge consists of blood effused from the inner surface of the uterus, and mixed with mucus from the uterus, vagina, and external parts of the generative apparatus. Being diluted by this admixture, the menstrual blood coagulates less perfectly than ordinary blood; and the frequent acidity of the vaginal mucus tends still further to diminish its coagulability. This has led to the erroneous supposition that the menstrual blood contains an unusually small quantity of fibrin, or none at all. The blood-corpuscles exist in it in their natural state: mixed with them may also be found numerous scales of epithelium derived from the mucous passages along which the discharge flows.

Corpus Luteum.

Immediately before, as well as subsequent to, the rupture of a Graafian vesicle, and the escape of its ovum, certain changes ensue in the interior of the vesicle, which result in the production of a yellowish mass, termed a *corpus luteum*.

When fully formed the corpus luteum of mammiferous

animals is a roundish solid body, of a yellowish or orange colour, and composed of a number of lobules, which surround, sometimes a small cavity, but more frequently a small stelliform mass of white substance, from which delicate processes pass as septa between the several lobules. Very often, in the cow and sheep, there is no white substance in the centre of the corpus luteum; and the lobules projecting from the opposite walls of the Graafian vesicle appear in a section to be separated by the thinnest possible lamina of semi-transparent tissue.

When a Graafian vesicle is about to burst and expel the ovum, it becomes highly vascular and opaque; and, immediately before the rupture takes place, its walls appear thickened on the interior by a reddish glutinous or fleshy-looking substance. Immediately after the rupture, the inner layer of the wall of the vesicle appears pulpy and flocculent. It is thrown into wrinkles by the contraction of the outer layer, and, soon, red fleshy mammillary processes grow from it, and granually enlarge till they nearly fill the vesicle, and even protrude from the orifice in the external covering of the ovary. Subsequently this orifice closes, but the fleshy growth within still increases during the earlier period of pregnancy, the colour of the substance gradually changing from red to yellow, and its consistence becoming firmer.

The corpus luteum of the human female (fig. 211) differs from that of the domestic quadruped in being of a firmer texture, and having more frequently a persistent cavity at its centre, and in the stelliform cicatrix, which remains in the cases where the cavity is obliterated, being proportionately of much larger bulk. The quantity of yellow substance formed is also much less: and, although the deposit increases after the vesicle has burst, yet it does not usually form mammillary growths projecting into the cavity of the vesicle, and never protrudes from the orifice, as is

the case in other Mammalia. It maintains the character of a uniform, or nearly uniform, layer, which is thrown into wrinkles, in consequence of the contraction of the external tunic of the vesicle. After the orifice of the vesicle has closed, the growth of the yellow substance continues during the first half of pregnancy, till the cavity is reduced to a comparatively small size, or is obliterated; in the latter case, nearly a white stelliform cicatrix remains in the centre of the corpus luteum.

Fig. 211.*

An effusion of blood generally takes place into the cavity of the Graafian vesicle at the time of its rupture, especially in the human subject; but it has no share in forming the yellow body; it gradually loses its colouring matter, and acquires the character of a mass of fibrin. The serum of the blood sometimes remains included within a cavity in the centre of the coagulum, and then the decolorized fibrin forms a membraniform sac, lining the corpus luteum. At

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Fig. 211. Corpora lutea of different periods. B. Corpus luteum of about the sixth week after impregnation, showing its plicated form at that period. 1. Substance of the ovary. 2. Substance of the corpus luteum. 3. A greyish coagulum in its cavity. After Dr. Paterson. A. Corpus luteum, two days after delivery. D. In the twelfth week after delivery. After Dr. Montgomery.

other times the serum is removed, and the fibrin constitutes a solid stelliform mass.

The yellow substance of which the corpus luteum consists, both in the human subject and in the domestic animals, is a growth from the inner surface of the Graafian vesicle, the result of an increased development of the cells forming the membrana granulosa, which naturally lines the internal tunic of the vesicle.

The first changes of the internal coat of the Graafian vesicle in the process of formation of a corpus luteum, seem to occur in every case in which an ovum escapes; as well in the human subject as in the domestic quadrupeds. If the ovum is impregnated, the growth of the yellow substance grows on during nearly the whole period of gestation, and forms the large corpus luteum commonly described as a characteristic mark of impregnation. If the ovum is not impregnated, the growth of yellow substance on the internal surface of the vesicle proceeds, in the human ovary, no further than the formation of a thin layer, which shortly disappears; but in the domestic animals it continues for some time after the ovum has perished, and forms a corpus luteum of considerable size. The fact, that a structure, in its essential characters similar to, though smaller than, a corpus luteum observed during pregnancy, is formed in the human subject, independent of impregnation or of sexual union, coupled with the varieties in size of corpora lutea formed during pregnancy, necessarily renders unsafe all evidence of previous impregnation founded on the existence of a corpus luteum in the ovary.

The following table by Dalton, expresses well the differences between the corpus luteum of the pregnant and unimpregnated condition respectively.

	Corpus Luteum of Menstruation.	Corpus Luteum of Pregnancy.
At the end of three weeks	Three-quarters of an inch in diameter; central clot reddish; convoluted wall pale.	
One month	Smaller; convoluted wall bright yellow; clot still reddish.	Larger; convoluted wall bright yellow; clot still reddish.
Two months	Reduced to the condition of an insignificant cicatrix.	Seven-eighths of an inch in diameter; convoluted wall bright yellow; clot perfectly decolorised.
Six months	Absent.	Still as large as at end of second month; clot fibrinous; convoluted wall paler.
Nine months	Absent.	One-half an inch in diameter; central clot converted into a radiating cicatrix; the external wall tolerably thick and convoluted, but without any bright yellow colour.

IMPREGNATION OF THE OVUM.

Male Sexual Functions.

The fluid of the male, by which the ovum is impregnated, consists essentially of the semen secreted by the testicles; and to this are added, as necessary, perhaps, to its perfection, a material secreted by the vesiculæ seminales, in which, as in reservoirs, the semen lies before its discharge, as well as the secretion of the prostate gland, and of Cowper's glands. Portions of these several fluids are, probably, all discharged, together with the proper secretion of the testicles.

The secreting structure of the testicle is disposed in two contiguous parts, (1) the body of the testicle enclosed within a tough fibrous membrane, the *tunica albuginea*, on the outer surface of which is the serous covering formed by the *tunica vaginalis*, and (2) the *epididymis*. The *vas deferens*,

the main trunk of the secreting tube, when followed back to its origin, is found to pass to the lower part of the epididymis, and assumes there a much less diameter with a very tortuous course: with its various convolutions it forms first the mass named *globus minor*, then the *body*, and then the *globus major* of the epididymis. At the last-named part, the duct divides into ten or twelve small branches, the convolutions of which form coniform masses, named *coni vasculosi*; and the vessels continued from these, the *vasa efferentia*, after anastomosing, one with another, in what is called the *rete testis*, lead finally through the *tubuli recti* or *vasa recta* to the tubules which form the proper substance of the testicle, wherein they are arranged in lobules, closely packed, and all attached to the tough fibrous tissue at the back of the testicle.

Fig. 212.*

The *seminal tubes*, or *tubuli seminiferi*, which compose the proper substance of the testicle, are fine thread-like tubules, formed of simple homogeneous membrane, measuring on an average $\frac{1}{100}$th to $\frac{1}{200}$th of an inch in diameter, and lined with epithelium or gland-cells. Rarely branching, they extend as simple tubes through a great length, with the same uniform structure, and probably terminate either in free closed extremities or in loops. Their walls are covered with fine capillary blood-vessels, through which, reckoning their great extent in

* Fig. 212. Plan of a vertical section of the testicle, showing the arrangement of the ducts. The true length and diameter of the ducts have been disregarded. *a*, *a*, tubuli seminiferi coiled up in the separate lobes; *b*, tubuli recti or vasa recta; *c*, rete testis; *d*, vasa efferentia ending in the coni vasculosi; *l*, *e*, *g*, convoluted canal of the epididymis; *h*, vas deferens; *f*, section of the back part of the tunica albuginea; *i*, *i*, fibrous processes running between the lobes; *s*, mediastinum.

A *Fig.* 213.* B

C

* Fig. 213. A, spermatic filaments from the human vas deferens (from Kölliker). 1, magnified 350 diameters; 2, magnified 800 diameters; *a*, from the side; *b*, from above. B, spermatic cells and spermatozoa of the bull undergoing development (from Kölliker) $\frac{450}{1}$. 1, spermatic cells, with one or two nuclei, one of them clear; 2, 3, free nuclei, with spermatic filaments forming; 4, the filaments elongated and the body widened; 5, filaments nearly fully developed. C, escape of the spermatozoa from their cells in the same animal. 1, spermatic cell containing the spermatozoon coiled up within it; 2, the cells elongated by the partial uncoiling of the spermatic filament; 3, a cell from which the filament has in part become free; 4, the same with the body also partially free; 5, spermatozoon from the epididymis with vestiges of the cell adherent; 6, spermatozoon from the vas deferens, showing the small enlargement, *b*, on the filament.

comparison with the size of the spermatic artery, the blood must move very slowly.

The *seminal fluid* secreted by the testicle is one of those secretions in which a process of development is continued after its formation by the secreting cells, and its discharge from them into the tubes. The principal part of this development consists in the formation of the peculiar bodies named *seminal filaments, spermatozoa* or *spermatozoids* (fig. 213) the complete development of which, in their full proportion of number, is not achieved till the semen has reached, or has for some time lain in, the vesiculæ seminales. Earlier, after its first secretion, the semen contains none of these bodies, but granules and round corpuscles (seminal corpuscles), like large nuclei, enclosed within parent-cells (fig. 213). Within reach of these corpuscles, or nuclei, a seminal filament is developed, by a similar process in nearly all animals. Each corpuscle, or nucleus, is filled with granular matter; this is gradually converted into a spermatozoid, which is at first coiled up, and in contact with the inner surface of the wall of the corpuscle (fig. 213, C, 1).

Thus developed, the human seminal filaments consist of a long, slender, tapering portion, called the body or tail, to distinguish it from the head, an oval or pyriform portion of larger diameter, flattened, and sometimes pointed. They are from $\frac{1}{500}$th to $\frac{1}{600}$th of an inch in length, the length of the head alone being from $\frac{1}{5000}$th to $\frac{1}{3000}$th of an inch, and its width about half as much. They present no trace of structure, or dissimilar organs; a dark spot often observed in the head, is probably due to its being concave, like a blood corpuscle. They move about in the fluid like so many minute corpuscles, with each a ciliary process, lashing their tails, and propelling their heads forwards in various lines. Their movement, which is probably essentially, as well as apparently, similar to that of ciliary processes, appears nearly independent of external

conditions, provided the natural density of the fluid is preserved; disturbing this condition, by either evaporating the semen or diluting it, will stop the movement. It may continue within the body of the female for seven or eight days, and out of the body for at least nearly twenty-four hours. The direction of the movement is quite uncertain: but in general, the current that each excites keeps it from the contact of others. The rate of motion, according to Valentin, is about one inch in thirteen minutes.

Respecting the purpose served by these seminal filaments, or concerning their exact nature, little that is certain can be said. Their occurrence in the impregnating fluid of nearly all classes of animals, proves that they are essential to the process of impregnation; but beyond this, and that their contact with the ovum is necessary for its development, nothing is known.

The seminal fluid is, probably, after the period of puberty, secreted constantly, though, except under excitement, very slowly, in the tubules of the testicles. From these it passes along the vasa deferentia into the vesiculæ seminales, whence, if not expelled in emission, it may be discharged, as slowly as it enters them, either with the urine, which may remove minute quantities, mingled with the mucus of the bladder and the secretion of the prostate, or from the urethra in the act of defecation.

The *vesiculæ seminales* have the appearance of out-growths from the vasa deferentia. Each vas deferens, just before it enters the prostate gland, through part of which it passes to terminate in the urethra, gives off a side-branch, which bends back from it at an acute angle; and this branch dilating, variously branching, and pursuing in both itself and its branches a tortuous course, constructs the vesicula seminalis. Each of the vesiculæ, therefore, might be unravelled into a single branching tube, sacculated, convoluted, and folded up.

The mucous membrane lining the vesiculæ seminales, like that of the gall-bladder, is minutely wrinkled and set with folds and ridges arranged so as to give it a finely reticulated appearance. The rest of their walls is formed, chiefly of a layer of organic muscular fibres, from which

Fig. 214.*

they derive contractile power for the expulsion of their contents.

To the vesiculæ seminales a double function may be assigned; for they both secrete some fluid to be added to

* Fig. 214. Dissection of the base of the bladder and prostate gland, showing the vesiculæ seminales and vasa deferentia (from Haller).—*a*, lower surface of the bladder at the place of reflexion of the peritoneum; *b*, the part above covered by the peritoneum; *i*, left vas deferens, ending in *e*, the ejaculatory duct; the vas deferens has been divided near *i*, and all except the vesicle portion has been taken away; *s*, left vesicula seminalis joining the same duct; *s*, *s*, the right vas deferens and right vesicula seminalis, which has been unravelled; *p*, under side of the prostate gland; *m*, part of the urethra; *u*, *u*, the ureters (cut short near *h*), the right one turned aside.

that of the testicles, and serve as reservoirs for the seminal fluid. The former is their most constant and probably most important office; for in the horse, bear, guinea-pig, and several other animals, in whom the vesiculæ seminales are large and of apparently active function, they do not communicate with the vasa deferentia, but pour their secretions, separately, though it may be simultaneously, into the urethra. In man, also, when one testicle is lost, the corresponding vesicula seminalis suffers no atrophy, though its function as a reservoir is abrogated. But how the vesiculæ seminales act as secreting organs is unknown; the peculiar brownish fluid which they contain after death does not properly represent their secretion, for it is different in appearance from anything discharged during life, and is mixed with semen. It is nearly certain, however, that their secretion contributes to the proper composition of the impregnating fluid; for in all the animals in whom they exist, and in whom the generative functions are exercised at only one season of the year, the vesiculæ seminales, whether they communicate with the vasa deferentia or not, enlarge commensurately with the testicles at the approach of that season.

That the vesiculæ are also reservoirs in which the seminal fluid may lie for a time previous to its discharge, is shown by their commonly containing the seminal filaments in larger abundance than any portion of the seminal ducts themselves do. The fluid-like mucus, also, which is often discharged from the vesiculæ in straining during defecation, commonly contains seminal filaments. But no reason can be given why this office of the vesiculæ should not be equally necessary to all the animals whose testicles are organized like those of man, or why in many animals the vesiculæ are wholly absent.

There is an equally complete want of information respecting the secretions of the prostate and Cowper's glands, their nature and purposes. That they contribute to

the right composition of the impregnating fluid, is show
both by the position of the glands and by their enlargin
with the testicles at the approach of an animal's breedin
time. But that they contribute only a subordinate part
shown by the fact, that, when the testicles are lost, thoug
these other organs be perfect, all procreative power ceases

The mingled secretions of all the organs just describe
form the semen or seminal fluid. Its corpuscles have bee
already described (p. 734): its fluid part has not bee
satisfactorily analysed: but Henle says it contains fibri
because shortly after being discharged, flocculi form in
by spontaneous coagulation, and leave the rest of
thinner and more liquid, so that the filaments move in
more actively.

Nothing has shown what it is that makes this fluid wit
its corpuscles capable of impregnating the ovum, or (wh
is yet more remarkable) of giving to the developing of
spring all the characters, in features, size, mental dispos
tion, and liability to disease, which belong to the fathe
This is a fact wholly inexplicable: and is, perhaps, onl
exceeded in strangeness by those facts which show th
the seminal fluid may exert such an influence, not only
the ovum which it impregnates, but, through the mediu
of the mother, on many which are subsequently impreg
nated by the seminal fluid of another male. It has bee
often observed, for example, that a well-bred bitch, if sh
have been once impregnated by a mongrel dog, will n
bear thorough-bred puppies in the next two or thre
litters after that succeeding the copulation with th
mongrel. But the best instance of the kind was in th
case of a mare belonging to Lord Morton, who, while h
was in India, wished to obtain a cross-breed between th
horse and quagga, and caused this mare to be covered by
a male quagga. The foal that she next bore had distinct
marks of the quagga, in the shape of its head, black bars
on the legs and shoulders, and other characters. After

this time she was thrice covered by horses, and every time the foal she bore had still distinct, though decreasing, marks of the quagga; the peculiar characters of the quagga being thus impressed not only on the ovum then impregnated, but on the three following ova impregnated by horses. It would appear, therefore, that the constitution of an impregnated female may become so altered and tainted with the peculiarities of the impregnating male, through the medium of the fœtus, that she necessarily imparts such peculiarities to any offspring she may subsequently bear by other males. Of the direct means by which a peculiarity of structure on the part of a male is thus transmitted, nothing whatever is known.

DEVELOPMENT.

Changes in the Ovum previous to the Formation of the Embryo.

Of the changes which the ovum undergoes previous to the formation of the embryo, some occur while it is still in the ovary, and are apparently independent of impregnation: others take place after it has reached the Fallopian tube. The knowledge we possess of these changes is derived almost exclusively from observations on the ova of mammiferous animals, especially the bitch and rabbit: but it may be inferred that analogous changes ensue in the human ovum.

Bischoff describes the yelk of an ovarian ovum after coitus as being unchanged in its characters, with the single exception of being fuller and more dense; it is still granular, as before, and does not possess any of the cells subsequently found in it. The germinal vesicle always disappears, sometimes before the ovum leaves the ovary, at other times not until it has entered the Fallopian tube; but always before the commencement of the metamorphosis of the yelk.

As the ovum approaches the middle of the Fallopian tube, it begins to receive a new investment, consisting of

a layer of transparent albuminous or glutinous substance, which forms upon the exterior of the zona pellucida. It is at first exceedingly fine, and, owing to this, and to its transparency, is not easily recognized: but at the lower part of the Fallopian tube it acquires considerable thickness.

Fig. 215.*

About this time, that it is to say, during its passage through the Fallopian tube, a very remarkable change takes place in the interior of the ovum. The whole yelk becomes constricted in the middle, and surrounded by a furrow, which, gradually deepening, at length cuts the yelk in half, while the same process begins almost immediately in each half of the yelk, and cuts it also in two. The same process is repeated in each of the quarters, and so on, until at last by continual cleavings the whole yelk is changed into a mulberry-like mass of small and more or less rounded bodies, sometimes called "vitelline spheres," the whole still enclosed by the *zona pellucida* or *vitelline membrane* (fig. 215). Each of these little spherules contains a transparent vesicle, like an oil-globule, which is seen with difficulty, on account of its being enveloped by the yelk-granules which adhere closely to its surface.

The cause of this singular subdivision of the yelk is

* Fig. 215. Diagrams of the various stages of cleavage of the yelk (after Dalton).

quite obscure: though the immediate agent in its production seems to be the central vesicle contained in each division of the yelk. Originally there was probably but one vesicle, situated in the centre of the entire granular mass of the yelk, and probably derived from the germinal vesicle. This, by some process of multiplication, divides and subdivides: then each division and subdivision attracts around itself, as a centre, a certain portion of the substance of the yelk.

About the time at which the mammiferous ovum reaches the uterus, the process of division and subdivision of the yelk appears to have ceased, its substance having been resolved into its ultimate and smallest divisions, while its surface presents a uniform finely-granular aspect, instead of its late mulberry-like appearance. The ovum, indeed, appears at first sight to have lost all trace of the cleaving process, and, with the exception of being paler and more translucent, almost exactly resembles the ovarian ovum, its yelk consisting apparently of a confused mass of finely granular substance. But on a more careful examination, it is found that these granules are aggregated into numerous minute spherical masses, each of which contains a clear vesicle in its centre, but is not, at this period, provided with an enveloping membrane, and possesses none of the other characters of a cell. The zona pellucida, and the layer of albuminous matter surrounding it, have at this time the same character as when at the lower part of the Fallopian tube.

The time occupied in the passage of the ovum, from the ovary to the uterus, occupies probably eight or ten days in the human female.

Shortly after this, important changes ensue. Each of the several globular segments of the yelk becomes surrounded by a membrane, and is thus converted into a cell, the nucleus of which is formed by the central vesicle, the contents by the granular matter originally composing the

globule: these granules usually arrange themselves concentrically around the nucleus. When the peripheral cells, which are formed first, are fully developed, they arrange themselves at the surface of the yelk into a kind of membrane, and at the same time assume a pentagonal or hexagonal shape from mutual pressure, so as to resemble pavement-epithelium. As the globular masses of the interior are gradually converted into cells, they also pass to the surface and accumulate there, thus increasing the thickness of the membrane already formed by the more superficial layer of cells, while the central part of the yelk remains filled only with a clear fluid. By this means the yelk is shortly converted into a kind of secondary vesicle, the walls of which are composed externally of the original vitelline membrane, and within by the newly formed cellular layer, the *blastodermic* or *germinal* membrane, as it is called. Very soon, however, the latter, by the development of new cells, increases in thickness, and splits into two layers, so that now the ovum has three coats. The vitelline membrane on the outside, and, within this, the *outer* and the *inner* layers of the blastodermic membrane.

Of the last-named layers, the superior or *outer*, which lies next to the zona pellucida or vitelline membrane, is called the *serous* layer; from it are developed the organs of the animal system of the body, *e.g.*, the bones, muscles, and integuments. The inferior or *inner* layer, in contact with the yelk itself, is named the *mucous* layer, and serves for the formation of the internal or visceral system of organs.

Changes of the Ovum within the Uterus.

Very soon after its formation, and division into two layers, the blastodermic vesicle or membrane presents at one point on its surface an opaque roundish spot, which is produced by an accumulation of cells and nuclei of cells, of less transparency than elsewhere. This space, the

"area germinativa" or germinal area, is the part at which the embryo first appears.

At first the area germinativa has a rounded form, but it soon loses this and becomes oval, then pear-shaped, and while this change in form is taking place, there gradually appears in its centre a clear space or *area pellucida* (fig. 216), bounded externally by a more opaque circle, the obscurity being due to the greater accumulation of nucleated cells and nuclei at that part than in the area pellucida.

*Fig. 216.**

The first trace of the embryo in the centre of the area pellucida consists of a shallow groove or channel, the *primitive groove* (fig. 216), formed of the external or serous fold of the germinal membrane, the groove being wider at its anterior or cephalic extremity, and tapering towards the opposite extremity.

Coincidently with the formation of the primitive groove, two oval masses of cells, the *laminæ dorsales*, appear, one on each side of the groove. At first scarcely elevated above the plane of the germinal membrane, they soon rise into two prominent masses, the upper borders of which gradually tend towards each other, turning inwards over the primitive groove. The parts from opposite sides then unite, and convert the primitive groove into a tube, large and rounded in front, narrow and lancet-shaped behind, which is the central canal of the cerebro-spinal axis, and contains the rudimental spinal cord and brain, which are developed in its interior (fig. 217).

* Fig. 216. (After Dalton.) Impregnated egg, with commencement of formation of embryo; showing the area germinativa or embryonic spot, the area pellucida, and the primitive groove or trace.

Immediately beneath, and in
primitive groove, may be seen,
narrow linear mass of cells, th
forms the basis around which t
are developed. The developmen

Fig. 217.*

indicated by the appearance of
distinct, plates, the rudiments c
which begin to appear at about t
lamina.

* Fig. 217. Portion of the germina
the embryo; from the ovum of a bitch.
yet closed, and at its upper or cephalic
B, which correspond to the three divisio
its lower extremity the groove presents
rhomboidalis) C. The margins of the
nerve-substance. Along the bottom of
streak, which is probably the chorda d
After Bischoff.

While the dorsal laminæ are closing over the primitive groove, thickened prolongations of the same *serous* layer are given off from the lower margin of each of them, and are named *laminæ viscerales seu ventrales.* These visceral laminæ by degrees bend downwards and inwards, and at length, enclosing a part of the yelk, unite and form the anterior walls of the trunk—enclosing the abdominal cavity below, as the dorsal plates enclose the cerebro-spinal canal above.

Fig. 218.*

Umbilical Vesicle.

The ventral laminæ, as they extend downwards and inwards, at first proceed on the same plane with the *inner* layer of the germinal membrane, which immediately lines them. Soon, however, they show a tendency to turn inwards, so as to constrict the yelk, and enclose only a part of it; and soon afterwards the yelk and the inner layer of the germinal membrane that contains it, are separated into two portions, one of which is retained within the body of the embryo, while the other remains outside, and receives the name of the *umbilical vesicle* (*v*, fig. 219). The cavity of the latter communicates for some time with that of the abdomen, through what is called the umbilicus, by means of a gradually narrowing canal, called the *vitelline duct;* the interior of the abdomen and that of the umbilical vesicle being lined by a continuous layer of the inner stratum, or *mucous* layer of the germinal membrane; while around both of them is a continuation of the outer, or *serous* layer

* Fig. 218. Diagram showing vascular area in the chick. *a*, Area pellucida. *b*, Area vasculosa. *c*, Area vitellina.

(fig. 219). From that portion of the mucous layer which is now enclosed within the body of the embryo, the intestinal canal is developed.

Fig. 219*.

Thus, by the constriction which the fold of germinal membrane, in which the abdominal walls are formed, produces at the umbilicus, the body of the embryo becomes

* Fig. 219. Diagrammatic section showing the relation in a mammal and in man between the primitive alimentary canal and the membranes of the ovum. The stage represented in this diagram corresponds to that of the fifteenth or seventeenth day in the human embryo, previous to the expansion of the allantois: *c*, the villous chorion; *a*, the amnion; *a'*, the place of convergence of the amnion and reflection of the false amnion *a'' a''*, or outer or corneous layer; *e*, the head and trunk of the embryo, comprising the primitive vertebræ and cerebro-spinal axis; *i*, *i*, the simple alimentary canal in its upper and lower portions; *v*, the yolk-sac or umbilical vesicle; *v i*, the vitello-intestinal opening; *u*, the allantois connected by a pedicle with the anal portion of the alimentary canal.

in great measure detached from the yelk sac or umbilical vesicle, though the cavity of the rudimentary intestine still communicates with it through the vitelline or omphalo-mesenteric duct, and contains part of the yelk substance with which the vesicle was filled. The yelk-sac contains, however, the greater part of the substance of the yelk, and furnishes a source whence nutriment is derived for the embryo. In birds, the contents of the yelk-sac afford nourishment until the end of incubation: but in Mammalia, the office of the corresponding umbilical vesicle ceases at a very early period, the quantity of yelk is small, and the embryo soon becomes independent of it by the connections it forms with the parent. Moreover, in birds, as the sac is emptied, it is gradually drawn into the abdomen through the umbilical opening, which then closes over it: but in Mammalia it always remains on the outside; and as it is emptied it contracts (fig. 220), shrivels up, and together with the part of its duct external to the abdomen, is detached and disappears either before, or at the termination of intra-uterine life, the period of its disappearance varying in different orders of Mammalia.

*Fig. 220.**

When blood-vessels begin to be developed, they ramify largely over the walls of the umbilical vesicle, and are actively concerned in absorbing its contents and conveying them away for the nutrition of the embryo.

The Amnion and Allantois.

At an early stage of development of the fœtus, and some time before the completion of the changes which have been just described, two important structures, called respectively

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* Fig. 220. Human embryo with umbilical vesicle; about the fifth week (after Dalton).

the *amnion* and the *allantois*, begi
nion being developed by the *extern*
the *internal* layer of the blastoder

Fig. 221.*

The amnio
lowing mann
of the blastod
up in the fo
body of the e
appears as if
pression, with
membrane ra
it. On section, the appearance
fig. 221.

Soon the edges of the fold r
above and around the embryo, c
double layer of membrane at their
absorbed, the two layers of which
made up are separated from each o
inner of the two forms the *amnion*,
with the integument of the fœtus
the *outer* layer, receding farther
forms one with the inner surface
membrane, which in the meantim
alterations to be immediately desc

As the term of pregnancy adva
more and more separated from the
considerable quantity of fluid, the

During the process of develop
allantois (*c*, fig. 222) begins to b
from, or near the hinder portion o
which it communicates, it is at fi
cells; but becoming vesicular and v
nous and vascular, it insinuates it
folds, just described, and comes

* Fig. 221. Diagram of fecundated
bilical vesicle; b, amniotic cavity; c, al

union with the outer of the two folds, which has itself, as before said, become one with the external investing membrane of the egg. As it grows, the allantois becomes exceedingly vascular, and in birds (fig. 222), envelopes the whole embryo—taking up vessels, so to speak, to the outer investing membrane of the egg, and lining the inner surface of the shell with a vascular membrane; by these means affording an extensive surface in which the blood may be aerated. In the human subject and in other mammalia, the vessels carried out by the allantois are distributed only to a special part of the outer membrane, at which a structure called the *placenta* is developed.

*Fig. 222.**

In Mammalia, as the visceral laminæ close in the abdominal cavity, the allantois is thereby divided at the umbilicus into two portions; the outer part, extending from the umbilicus to the *chorion* (p. 751), soon shrivelling; while the inner part, remaining in the abdomen, is in part converted into the urinary bladder; the portion of the inner part not so converted, extending from the bladder to the umbilicus, under the name of the *urachus*. After birth the umbilical cord, and with it the external and shrivelled portion of the allantois, are cast off at the umbilicus, while the *urachus* remains as an impervious cord stretched from the top of the urinary bladder to the umbilicus, in the middle line of the body, immediately beneath the parietal layer of the peritoneum. It is sometimes enumerated among the ligaments of the bladder.

* Fig. 222. Fecundated egg with allantois nearly complete. *a*, inner layer of amniotic fold; *b*, outer layer of ditto; *c*, point where the amniotic folds come in contact. The allantois is seen penetrating between the outer and inner layers of the amniotic folds. This figure, which represents only the amniotic folds and the parts within them, should be compared with figs. 223, 224, in which will be found the structures external to these folds.

It must not be supposed that the phenomena which have been successively described, occur in any regular order one after another. On the contrary, the development of one part is going on side by side with that of another.

Fig. 223. *Fig.* 224.

Development of Blood-vessels.

At an early period of development, and during the changes just described, an accumulation of cells ensues between the mucous and serous laminæ at a part of the germinal membrane named the *area vasculosa* (*b*, fig. 218). Within this mass, which constitutes a third or middle layer of the blastodermic membrane, is laid the foundation for the development of the vascular system. At the circumference of the vascular area, insulated red spots and lines make their appearance, and these soon unite, so as to form a network of vessels filled with blood. The margin of the vascular layer is at first limited and quite circular, being bounded by vessels united in a *circulus venosus*, or *sinus terminalis*,

* Figs. 223 and 224 (after Todd and Bowman). *a*, chorion with villi. The villi are shown to be best developed in the part of the chorion to which the allantois is extending; this portion ultimately becomes the placenta. *b*, space between the two layers of the amnion. *c*, amniotic cavity. *d*, situation of the intestine, showing its connexion with the umbilical vesicle. *e*, umbilical vesicle. *f*, situation of heart and vessels. *g*, allantois.

but it soon extends over the whole surface of the germinal membrane.

At about the same time, the rudimentary heart is formed in the same layer of the germinal membrane. As shown by Schwann, the blood-vessels are developed originally from nucleated cells. These cells send out processes; the processes from different cells unite; and in this way ramifications and a network are produced—vessels extending from this network in the area vasculosa into the area pellucida, and joining the rudimentary heart (see p. 765).

The Chorion.

It has been already remarked that the *allantois* is a structure which extends from the body of the fœtus to the outer investing membrane of the ovum, that it insinuates itself between the two layers of the amniotic fold, and becomes fused with the outer layer, which has itself become previously fused with the vitelline membrane. By these means the external investing membrane of the ovum, or the *chorion*, as it is now called, represents three layers, namely, the original vitelline membrane, the outer layer of the amniotic fold, and the allantois.

Fig. 225.

Very soon after the entrance of the ovum into the uterus, in the human subject, the outer surface of the chorion is found beset with fine processes, the so-called *villi of the chorion* (*a*, figs. 223, 224), which give it a rough and shaggy appearance. At first only cellular in structure, these little outgrowths subsequently become vascular by the development in them of loops of capillaries (fig. 225); and the latter at length form the minute extremities of the blood-vessels which are, so to speak, conducted from the fœtus to the

chorion by the allantois. The function of the villi of the chorion is evidently the absorption of nutrient matter for the fœtus; and this is probably supplied to them at first from the fluid matter secreted by the follicular glands of the uterus, in which they are soaked. Soon, however, the fœtal vessels of the villi come into more intimate relation with the vessels of the uterus. The part at which this relation between the vessels of the fœtus and those of the parent ensues, is not, however, over the whole surface of the chorion: for, although all the villi become vascular, yet they become indistinct or disappear except at one part where they are greatly developed, and by their branching give rise, with the vessels of the uterus, to the formation of the *placenta*.

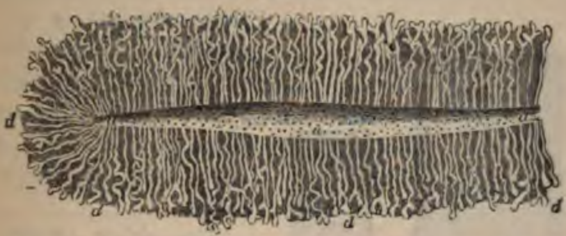
To understand the manner in which the *fœtal* and *maternal* blood-vessels come into relation with each other in the placenta, it is necessary briefly to notice the changes which the uterus undergoes after impregnation. These changes consist especially of alterations in structure of the superficial part of the mucous membrane which lines the interior of the uterus, and which forms, after a kind of development to be immediately described, the *membrana decidua*, so called on account of its being discharged from the uterus at the period of parturition.

Changes of the Mucous Membrane of the Uterus, and Formation of the Placenta.

The mucous membrane of the human uterus is abundantly beset with tubular follicles, arranged perpendicularly to the surface. These follicles are very small in the unimpregnated uterus; but when examined shortly after impregnation, they are found elongated, enlarged, and much waved and contorted towards their deep and closed extremity, which is implanted at some depth in the tissue of the uterus, and commonly dilates into two or three closed sacculi (fig. 226).

According to Dr. Sharpey, the glands of the mucous membrane of the bitch's uterus (and according to H. Müller, that of the human female also) are of two kinds,

Fig. 226.*



simple and compound. The former, which are the more numerous, are merely very short unbranched tubes closed at one end (fig. 227,[1],[1]), the latter ([2],[2]) have a long duct dividing into convoluted branches; both open on the inner surface of the membrane by small round orifices, lined with epithelium and set closely together.

Fig. 227.†

On the internal surface of the mucous membrane may be seen the circular orifices of the glands, many of which are, in the early period of pregnancy, surrounded by a whitish ring, formed of the epithelium which lines the follicles (fig. 228).

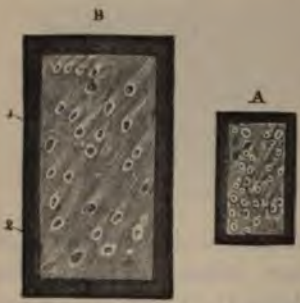
Coincidently with the increasing size of the follicles, the quantity of their secretion is augmented, the vessels of

* Fig. 226. Section of the lining membrane of a human uterus at the period of commencing pregnancy, showing the arrangement and other peculiarities of the glands, *d*, *d*, *d*, with their orifices, *a*, *a*, *a*, on the internal surface of the organ. Twice the natural size.

† Fig. 227. A vertical section of the mucous membrane, showing uterine glands of the bitch, magnified twelve diameters; 1, 1, simple glands; 2, 2, compound ditto (from Sharpey).

the mucous membrane become larger and more numerous, while a substance composed chiefly of nucleated cells fill up the interfollicular spaces in which the blood-vessels are contained. The effect o these changes is an in creased thickness, softness and vascularity of the mu cous membrane, the super ficial part of which itsel forms the *membrana de cidua.*

Fig. 228.*



The object of this in creased development seem to be the production o nutritive materials for th ovum; for the cavity of the uterus shortly becomes fille with secreted fluid, consisting almost entirely of nucleate cells, in which the villi of the chorion are embedded.

When the ovum first enters the uterus it becomes im bedded in the structure of the decidua, which is yet quit soft, and in which soon afterwards three portions are dis tinguishable. These have been named the decidua *vera*, th decidua *reflexa*, and the decidua *serotina*. The first of these the decidua *vera*, lines the cavity of the uterus; the second or decidua *reflexa*, is a part of the decidua vera, whic grows up around the ovum, and, wrapping it closely, form its immediate investment. The third, or decidua *serotina* is the part of the decidua vera which becomes especiall developed in connection with those villi of the chorion which, instead of disappearing, remain to form the fœtal part of the *placenta*.

* Fig. 228. Two thin segments of human decidua after recent im pregnation, viewed on a dark ground : they show the openings on the surface of the membrane. A is magnified six diameters, and B twelve diameters. At 1, the lining of epithelium is seen within the orifices, at 2 it has escaped (from Sharpey).

As the ovum increases in size, the decidua vera and the decidua reflexa gradually come into contact, and in the third month of pregnancy the cavity between them has quite disappeared. Henceforth it is very difficult, or even impossible, to distinguish the two layers.

During these changes the deeper part of the mucous membrane of the uterus, at and near the region where the placenta is placed, becomes hollowed out by sinuses, or cavernous spaces, which communicate on the one hand with arteries and on the other with veins of the uterus. Into these sinuses the villi of the chorion protrude, pushing the thin wall of the sinus before them, and so come into intimate relation with the blood contained in them. There is no direct communication between the blood-vessels of the mother and those of the fœtus; but the layer or layers of membrane intervening between the blood of the one and of the other offer no obstacle to a free interchange of matters between them. Thus the villi of the chorion, containing fœtal blood, are bathed or soaked in maternal blood contained in the uterine sinuses. The arrangement may be roughly compared to filling a glove with fœtal blood, and dipping its fingers into a vessel containing maternal blood. But in the fœtal villi there is a constant stream of blood into and out of the loop of capillary blood-vessel contained in it, as there is also into and out of the maternal sinuses.

It would seem from the observations of Professor Goodsir, that, at the villi of the placental tufts, where the fœtal and maternal portions of the placenta are brought into close relation with each other, the blood in the vessels of the mother is separated from that in the vessels of the fœtus by the intervention of two distinct sets of nucleated cells (fig. 229). One of these (*b*) belongs to the maternal portion of the placenta, is placed between the membrane of the villus and that of the vascular system of the mother, and is probably designed to separate from the blood of the

parent the materials destined for the blood of the fœtus; the other (f) belongs to the fœtal portion of the placenta, is situated between the membrane of the villus and the loop of vessels contained within, and probably serves for the absorption of the material secreted by the other sets of cells, and for its conveyance into the blood-vessels of the fœtus. Between the two sets of cells with their investing membrane there exists a space (d), into which it is probable that the materials secreted by the one set of cells of the villus are poured in order that they may be absorbed by the other set, and thus conveyed into the fœtal vessels.

*Fig. 229.**

Not only, however, is there a passage of materials from the blood of the mother into that of the fœtus, but there can be no doubt of the existence of a mutual interchange of materials between the blood both of fœtus and of parent, the latter supplying the former with nutriment, and in turn abstracting from it materials which require to be removed. Dr. Alexander Harvey's experiments were very decisive on this point. The view has also received abundant support of late from Mr. Hutchinson's important observations on the communication of syphilis from the father to the mother, through the instrumentality of the fœtus; and still more from Mr. Savory's experimental researches, which prove quite clearly that the female parent may be directly inoculated through the fœtus. Having opened the abdomen and uterus of a pregnant bitch, Mr. Savory injected a solution

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* Fig. 229. Extremity of a placental villus. *a*, lining membrane of the vascular system of the mother; *b*, cells immediately lining *a*; *d*, space between the maternal and fœtal portions of the villus; *e*, internal membrane of the villus, or external membrane of the chorion; *f*, internal cells of the villus, or cells of the chorion; *g*, loop of umbilical vessels (after Goodsir).

of strychnia into the abdominal cavity of one fœtus, and into the thoracic cavity of another, and then replaced all the parts, every precaution being taken to prevent escape of the poison. In less than half an hour, the bitch died from tetanic spasms; the fœtuses operated on were also found dead, while the others were alive and active. The experiments, repeated on other animals with like results, leave no doubt of the rapid and direct transmission of matter from the fœtus to the mother, through the blood of the placenta.

The placenta, therefore, of the human subject is composed of a *fœtal* part and a *maternal* part,—the term, placenta, properly including all that entanglement of fœtal villi and maternal sinuses, by means of which the blood of the fœtus is enriched and purified after the fashion necessary for the proper growth and development of those parts which it is destined to nourish.

The whole of this structure is not, as might be imagined, thrown off immediately after birth. The greater part, indeed, comes away at that time, as the *after-birth*, and the separation of this portion takes place by a rending or crushing through of that part at which its cohesion is least strong, namely, where it is most burrowed and undermined by the cavernous spaces before referred to. In this way it is cast off with the fœtal membranes and the decidua *vera* and *reflexa*, together with a part of the decidua *serotina*. The remaining portion withers, and disappears by being gradually either absorbed, or thrown off in the uterine discharges or the *lochia*, which occur at this period.

A new mucous membrane is of course gradually developed, as the old one, by its peculiar transformation into what is called the decidua, ceases to perform its original functions.

The *umbilical cord*, which in the latter part of fœtal life is almost solely composed of the two arteries and the single vein which respectively convey fœtal blood to and from the

placenta, contains the remnants of other structures which in the early stages of the development of the embryo were, as already related, of great comparative importance. Thus, in early fœtal life, it is composed of the following parts:—(1). Externally, a layer of the amnion, reflected over it from the umbilicus. (2). The umbilical vesicle with its duct and appertaining omphalo-mesenteric blood-vessels. (3). The remains of the allantois, and continuous with it the urachus. (4). The umbilical vessels, which, as just remarked, ultimately form the greater part of the cord.

DEVELOPMENT OF ORGANS.

It remains now to consider in succession the development of the several organs and systems of organs in the further progress of the embryo.

Development of the Vertebral Column and Cranium.

The primitive part of the vertebral column in all the Vertebrata is the gelatinous chorda dorsalis, which consists entirely of cells. This cord tapers to a point at the cranial and caudal extremities of the animal. In the progress of its development, it is found to become enclosed in a membranous sheath, which at length acquires a fibrous structure, composed of transverse annular fibres. The chorda dorsalis is to be regarded as the azygos axis of the spinal column, and, in particular, of the future bodies of the vertebræ, although it never itself passes into the cartilaginous or osseous state, but remains enclosed as in a case within the persistent parts of the vertebral column which are developed around it. It is permanent, however, only in a few animals: in the majority it disappears at an early period.

The cartilaginous or osseous vertebræ are always first developed in pairs of lateral elements at the sides of the

chorda dorsalis. From these lateral elements are formed the bodies and the arches of the vertebræ. In some animals, as the sturgeon, however, the lateral elements of the vertebræ undergo no further development, and it is here that the chorda dorsalis is persistent through life. In the myxinoid fishes the spinal column presents no vertebral segments, and there exists merely the chorda dorsalis with the fibrous layer surrounding its sheath, which is the layer in which the skeleton originates. This fibrous layer also forms superiorly the membranous covering of the vertebral canal.

In reptiles, birds, and mammals, the mode in which the vertebræ are formed around the chorda dorsalis seems to be different. When the formation of these parts from the blastema commences, there appears at each side of the chorda dorsalis a series of quadrangular figures, the rudiments of the future vertebræ. These gradually increase in number and size, so as to surround the chorda both above and below, sending out, at the same time, superiorly, processes to form the arches destined to enclose the spinal cord. In this primitive condition the body and arches of each vertebra are formed by one piece on each side. At a certain period these two primary elements, which have become cartilaginous, unite inferiorly by a suture. The chorda is now enclosed in a case, formed by the bodies of the vertebræ, but it gradually wastes and disappears. Before the disappearance of the chorda, the ossification of the bodies and arches of the vertebræ begins at distinct points.

The ossification of the body of a vertebra is first observed at the point where the two primitive elements of the vertebræ have united inferiorly. Those vertebræ which do not bear ribs, such as the cervical vertebræ, have generally an additional centre of ossification in the transverse process, which is to be regarded as an abortive rudiment of a rib. In the fœtal bird, these additional

ossified portions exist in all the cervical vertebræ, and gradually become so much developed in the lower part of the cervical region as to form the upper false ribs of this class of animals. The same parts exist in mammalia and man; those of the last cervical vertebræ are the most developed, and in children may, for a considerable period, be distinguished as a separate part on each side, like the root or head of a rib.

The true cranium is a prolongation of the vertebral column, and is developed at a much earlier period than the facial bones. Originally, it is formed of but one mass, a cerebral capsule, the chorda dorsalis being continued into its base, and ending there with a tapering point. This relation of the chorda dorsalis to the basis of the cranium is persistent through life in some fish, *e.g.*, the sturgeon. The first appearance of a solid support at the base of the cranium observed by Müller in fish, consists of two elongated bands of cartilage, one on the right and the other on the left side, which are connected with the cartilaginous capsule of the auditory apparatus, and united with each other in an arched manner anteriorly beneath the anterior end of the cerebral capsule. Hence, in the cranium, as in the spinal column, there are at first developed at the sides of the chorda dorsalis two symmetrical elements, which subsequently coalesce, and may wholly enclose the chorda.*

Development of the Face and Visceral Arches.

It has been said before that at an early period of development of the embryo, there grow up on the sides of the primitive groove the so-called *dorsal laminæ*, which at

* For much new and original matter relating to the development of the cranium, the reader is referred to the important lectures on Comparative Anatomy, delivered at the College of Surgeons by Professor Huxley.

length coalesce, and complete by their union the spinal canal. The same process essentially takes place in the head, so as to enclose the cranial cavity.

The so-called *visceral laminæ* have been also described as passing forwards, and gradually coalescing in front, as the dorsal laminæ do behind, and thus enclosing the thoracic and abdominal cavity. An analogous process occurs in the facial and cervical regions, but the enclosing laminæ, instead of being simple, as in the former instances, are cleft.

Fig. 230*

A

B

In this way the so-called visceral *arches* and *clefts* are formed, four on each side (fig. 230 A), and from or in connection with these arches the following parts are developed :—

From the *first* arch, and its maxillary process, the *superior maxillary*, the *palate* bone, and the *internal pterygoid* plate of the *sphenoid* bone, the *incus* and *malleus* and the *lower jaw*. The upper part of the face in the middle line is developed from the so-called *fronto-nasal* process (A, 3, fig. 230). From the *second* arch are developed the *stapes*, the *stapedius* muscle, the styloid process of the *temporal* bone,

* Fig. 230A. Magnified view from before of the head and neck of a human embryo of about three weeks (from Ecker)—1, anterior cerebral vesicle or cerebrum ; 2, middle ditto ; 3, middle or fronto-nasal process ; 4, superior maxillary process ; 5, eye ; 6, inferior maxillary process, or first visceral arch, and below it the first cleft ; 7, 8, 9, second, third, and fourth arches and clefts. B, anterior view of the head of a human fœtus of about the fifth week (from Ecker, as before, fig. IV.). 1, 2, 3, 5, the same parts as in A ; 4, the external nasal or lateral frontal process ; 6, the superior maxillary process ; 7, the lower jaw ; ×, the tongue ; 8, first branchial cleft becoming the meatus auditorius externus.

the *stylo-hyoid* ligament, and the *smaller cornu* of the *hyoid* bone. From the *third* visceral arch, the *greater cornu* and *body* of the hyoid bone. In man and other mammalia the *fourth* visceral arch is indistinct.

Development of the Extremities.

The extremities are developed in an uniform manner in all vertebrate animals. They appear in the form of leaf-like elevations from the parietes of the trunk (see fig. 231), at points where more or less of an arch will be produced for them within. The primitive form of the ex-

Fig. 231.*

tremity is nearly the same in all Vertebrata, whether it be destined for swimming, crawling, walking, or flying. In the human fœtus the fingers are at first united, as if webbed for swimming; but this is to be regarded not so

* Fig. 231. A human embryo of the fourth week, 3½ lines in length. 1, the chorion; 3, part of the amnion; 4, umbilical vesicle with its long pedicle passing into the abdomen; 7, the heart; 8, the liver; 9, the visceral arch destined to form the lower jaw, beneath which are two other visceral arches separated by the branchial clefts: 10, rudiment of the upper extremity; 11, that of the lower extremity; 12, the umbilical cord; 15, the eye; 16, the ear; 17, the cerebral hemispheres; 18, the optic lobes or corpora quadrigemina.

much as an approximation to the form of aquatic animals, as the primitive form of the hand, the individual parts of which subsequently become more completely isolated.

Development of the Vascular System.

The first development of the vascular system and heart in the germinal membrane has been already alluded to (p. 750) The earliest form of the heart presents itself as a solid compact mass of embryonic cells, similar to those of which the other organs of the body are constituted. It is at first unprovided with a cavity; but this shortly makes its appearance, resulting apparently from the separation from each other of the cells of the central portion. A liquid is now formed in the still closed cavity, and the central cells may be seen floating within it. These contents of the cavity are soon observed to be propelled to and fro with a tolerable degree of regularity, owing to the commencing pulsations of the heart. These pulsations take place even before the appearance of a cavity, and immediately after the first 'laying down' of the cells from which the heart is formed. At first they seldom exceed from fifteen to eighteen in the minute. The fluid within the cavity of the heart shortly assumes the characters of blood. At the same time the cavity itself forms a communication with the great vessels in contact with it, and the cells of which its wall are composed are transformed into fibrous and muscular tissues, and into epithelium.

Blood-vessels appear to be developed in two ways, according to the size of the vessels. In the formation of large blood-vessels, masses of embryonic cells similar to those from which the heart and other structures of the embryo are developed, arrange themselves in the position, form, and thickness of the developing vessel. Shortly afterwards the cells in the interior of a column of this kind seem to be developed into blood-corpuscles, while the

external layer of cells is converted into the walls of the vessel.

In the development of capillaries another plan is pur-

Fig. 232.

* Fig. 232. Capillary blood-vessels of the tail of a young larval frog. Magnified 350 times (after Kölliker).—*a*, capillaries permeable to blood ; *b*, fat-granules attached to the walls of the vessels, and concealing the nuclei ; *c*, hollow prolongation of a capillary, ending in a point ; *d*, a branching cell with nucleus and fat-granules ; it communicates by three branches with prolongation of capillaries already formed ; *e*, *e*, blood-corpuscles still containing granules of fat.

sued. This has been well illustrated by Kölliker, as observed in the tails of tadpoles. The first lateral vessels of the tail have the form of simple arches, passing between the main artery and vein, and are produced by the junction of prolongations, sent from both the artery and vein, with certain elongated or star-shaped cells, in the substance of the tail. When these arches are formed and are permeable to blood, new prolongations pass from them, join other radiated cells, and thus form secondary arches. In this manner, the capillary net-work extends in proportion as the tail increases in length and breadth, and it, at the same time, becomes more dense by the formation, according to the same plan, of fresh vessels within its meshes. The prolongations by which the vessels communicate with the star-shaped cells, consist at first of narrow-pointed projections from the side of the vessels, which gradually elongate until they come in contact with the radiated processes of the cells. The thickness of such a prolongation often does not exceed that of a fibril of fibrous tissue, and at first it is perfectly solid; but, by degrees, especially after its junction with a cell, or with another prolongation, or with a vessel already permeable to blood, it enlarges, and a cavity then forms in its interior (see fig. 232). With Kölliker's account, our own observations, made on the fine gelatinous tissue conveying the umbilical vessels of a sheep's embryo to the uterine cotyledons, completely accord. This tissue is well calculated to illustrate the various steps in the development of blood-vessels from elongating and branching cells.

About the time that the heart at its lowest extremity, receives the venous trunks, and at its upper extremity gives off the large arterial trunk, it becomes curved from a straight into a horse-shoe form, and shortly divides into three cavities (fig. 233). Of these three cavities, which are developed in all Vertebrata, the most posterior is the simple auricle; the middle one the simple ventricle; and the

most anterior the bulbus arteriosus. These three parts of the heart contract in succession. The auricle and the bulbus arteriosus at this period lie at the extremities of the horse-shoe. The bulging out of the middle portion inferiorly gives the first indication of the future form of the ventricle (see fig. 233). The great curvature of the horse-

Fig. 233.*

shoe by the same means becomes much more developed than the smaller curvature between the auricle and bulbus; and the two extremities, the auricle and bulb, approach each other superiorly, so as to produce a greater resemblance to the latter form of the heart, whilst the ventricle becomes more and more developed inferiorly. The heart of fishes retains these three cavities, no further division by internal septa into right and left chambers taking place. In Amphibia, also, the heart throughout life consists of the three muscular divisions which are so early formed in the embryo; but the auricle is divided internally by a septum into a pulmonary and systemic auricle. In reptiles, not merely the auricle is thus divided into two cavities, but a similar septum is more or less developed in the ventricle. In birds, mammals, and the human subject, both auricle and ventricle undergo complete division by septa; whilst in these animals as well as in reptiles, the bulbus aortæ is not permanent, but becomes lost in the ventricles. The septum dividing the ventricle commences at the apex and extends upwards. When it is complete, a septum is developed in the bulbus aortæ, separating the roots of the

* Fig. 233. Heart of the chick at the 45th, 65th, and 85th hours of incubation. 1, the venous trunks; 2, the auricle; 3, the ventricle; 4, the bulbus arteriosus (after Dr. Allen Thomson).

proper aorta and the pulmonary artery. The septum of the auricles is developed from a semilunar fold, which extends from above downwards. In man, the septum between the ventricles, according to Meckel, begins to be formed about the fourth week, and at the end of eight weeks is complete. The septum of the auricles, in man and all animals which possess it, remains imperfect throughout fœtal life. When the partition of the auricles is first commencing, the two venæ cavæ have different relations to the two cavities. The superior cava enters, as in the adult, into the right auricle; but the inferior cava is so placed that it appears to enter the left auricle, and the posterior part of the septum of the auricles is formed by the Eustachian valve, which extends from the point of entrance of the inferior cava. Subsequently, however, the septum, growing from above downwards, becomes directed more and more to the left of the vena cava inferior. During the entire period of fœtal life, there remains an opening in the septum, which the valve of the foramen ovale, developed in the third month imperfectly closes.

Circulation of Blood in the Fœtus.

The circulation of blood in the fœtus is peculiar, and differs considerably from that of the adult. It will be well, perhaps, to begin its description by tracing the course of the blood, which, after being carried out to the placenta by the two umbilical *arteries*, has returned, cleansed and replenished, to the fœtus by the umbilical vein.

It is at first conveyed to the under surface of the liver, and there the stream is divided,—a part of the blood passing straight on to the *inferior* vena cava, through a venous canal called the *ductus venosus*, while the remainder passes into the portal vein, and reaches the inferior vena cava only after circulating through the liver. Whether, however, by the direct route through the ductus venosus

auricle by the *superior* vena cava. It might be naturally expected that the two streams of blood would be mingled in the right auricle, but such is not the case, or only to a slight extent. The blood from the *superior* vena cava,—the less pure fluid of the two—passes almost exclusively into the *right* ventricle, through the auriculo-ventricular opening, just as it does in the adult; while the blood of the *inferior* vena cava is directed by a fold of the lining membrane of the heart, called the *Eustachian valve*, through the foramen ovale into the *left* auricle, whence it passes into the *left* ventricle, and out of this into the aorta, and thence to all the body. The blood of the *superior* vena cava, which, as before said, passes into the right ventricle, is sent out thence in small amount through the pulmonary artery to the lungs, and thence to the *left* auricle, as in the adult. The greater part, however, by far, does not go to the lungs, but instead, passes through a canal, the *ductus arteriosus*, leading from the pulmonary artery into the aorta just below the origin of the three great vessels which supply the upper parts of the body; and there meeting that part of the blood of the inferior vena cava which has not gone into these large vessels, it is distributed with it to the trunk and lower parts,—a portion passing out by way of the two umbilical *arteries* to the placenta. From the placenta it is returned by the umbilical *vein* to the under surface of the liver, from which the description started.

After birth the foramen ovale closes, and so do the ductus arteriosus and ductus venosus, as well as the umbilical vessels; so that the two streams of blood which arrive at the right auricle by the superior and inferior vena cava respectively, thenceforth mingle in this cavity of the heart, and passing into the right ventricle, go by way of the pulmonary artery to the lungs, and through these, after purification, to the left auricle and ventricle, to be distributed over the body. (See chapter on Circulation.)

Development of the Nervous System.

The mode in which the rudimentary structures of the cerebro-spinal nervous system are formed, has been already stated (p. 743). The dorsal laminæ, the inner borders of which close in and form the canal of the spinal cord, seem to leave a fissure in the situation of the medulla oblongata. Between this and the most anterior extremity of the canal, three vesicular enlargements, the vesicles of the brain, are developed (see fig. 217), and from these again are developed the following parts :—

From the *anterior* primary vesicle—the optic thalami, corpora striata, the third ventricle, and the cerebral hemispheres, together with some other parts in connection with those above named, as the corpus callosum, fornix, etc.

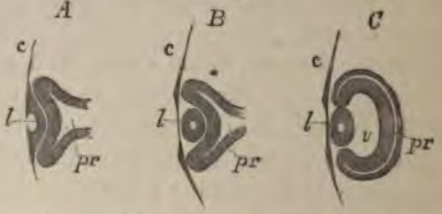
From the *middle* primary vesicle—the corpora quadrigemina and crura cerebri, with the aqueduct of Sylvius.

From the *posterior* primary vesicle—the cerebellum, pons Varolii, medulla oblongata, etc.

Development of the Organs of Sense.

The eye is in part developed as a protruded portion of the first primary cerebral vesicle; while passing backwards, and pressing on the front of this process or *primary optic*

Fig. 235.*



* Fig. 235. Longitudinal section of the primary optic vesicle in the chick magnified (from Remak).—A, from an embryo of sixty-five hours; B, a few hours later; C, of the fourth day; *c*, the corneous layer or epidermis, presenting in A, the open depression for the lens, which is

vesicle, is a pouch of the common integument, which subsequently becomes a shut sac, and in which is developed the lens and its capsule (fig. 236). Subsequently there is

Fig. 236.*

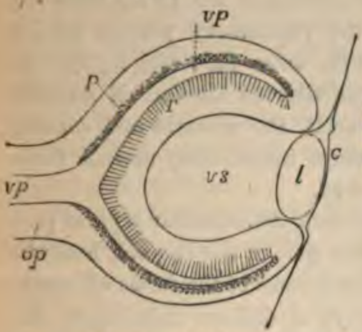


Fig. 237.†

protruded from below upwards, between the lens in front and the primary optic vesicle behind, another process or

closed in B and C; *l*, the lens follicle and lens; *pr*, the primary optic vesicle; in A and B, the pedicle is shown; in C, the section being to the side of the pedicle, the latter is not shown: *v*, the secondary ocular vesicle and vitreous humour.

* Fig. 236. Diagrammatic sketch of a vertical longitudinal section through the eyeball of a human fœtus of four weeks (after Kölliker) $\frac{100}{1}$. The section is a little to the side, so as to avoid passing through the ocular cleft: *c*, the cuticle where it becomes later the cornea; *l*, the lens; *o, p*, optic nerve formed by the pedicle of the primary optic vesicle; *v p*, primary medullary cavity or optic vesicle; *p*, the pigment layer of the choroid coat of the outer wall; *r*, the inner wall forming the retina; *v s*, secondary optic vesicle containing the rudiment of the vitreous humour.

† Fig. 237. Transverse vertical section of the eyeball of a human embryo of four weeks (from Kölliker) $\frac{100}{1}$. The anterior half of the section is represented: *p, r*, the remains of the cavity of the primary optic vesicle; *p*, the inner part of the outer layer forming the choroidal pigment; *r*, the thickened inner part giving rise to the columnar and other structures of the retina; *v*, the commencing vitreous humour within the secondary optic vesicle; *v'*, the ocular cleft through which the loop of the central blood-vessel, *a*, projects from below; *l*, the lens with a central cavity.

pouch, remaining for some time imperfect below, and called the *secondary optic vesicle*. The deficiency below contracts into what is called the *ocular cleft*, which subsequently becomes entirely obliterated. In connection with the *primary optic vesicle* are developed the retina from the invaginated portion, and the pigmentary portion of the choroid in connection with the outer part (fig. 236). In the *secondary* optic vesicle the vitreous humour is formed. The outer walls of the eyeball, the sclerotic and cornea, are developed from the tissues immediately around those which have been just described.

The iris is formed rather late, as a circular septum projecting inwards, from the fore part of the choroid, between the lens and the cornea. In the eye of the fœtus of Mammalia, the pupil is closed by a delicate membrane, the *membrana pupillaris*, which forms the front portion of a highly vascular membrane that, in the fœtus, surrounds

Fig. 238.*

the lens, and is named the *membrana capsulo pupillaris*. It

* Fig. 238. Blood-vessels of the capsulo-pupillary membrane of a new-born kitten, magnified (from Kölliker). The drawing is taken from a preparation injected by Tiersch, and shows in the central part the convergence of the net-work of vessels in the pupillary membrane.

is supplied with blood by a branch of the *arteria centralis retinæ*, which, passing forwards to the back of the lens, there subdivides. The membrana capsulo-pupillaris withers and disappears in the human subject a short time before birth.

The eyelids of the human subject and mammiferous animals, like those of birds, are first developed in the form of a ring. They then extend over the globe of the eye until they meet and become firmly agglutinated to each other. But before birth, or in the Carnivora after birth, they again separate.

The *ear* likewise, according to Huschke, consists of a part developed from within, and of one formed externally. The labyrinth is developed upon the hollow protruded part of the brain which forms the auditory nerve. It appears first in the form of an elongated vesicle at the hinder part of the head of very young embryoes above the second so-named branchial cleft. From it is developed a second vesicle, the rudiment of the cochlea, the convolutions of which are then formed. The semicircular canals are produced, as diverticula of the vestibule, which terminate by again communicating with the same cavity.

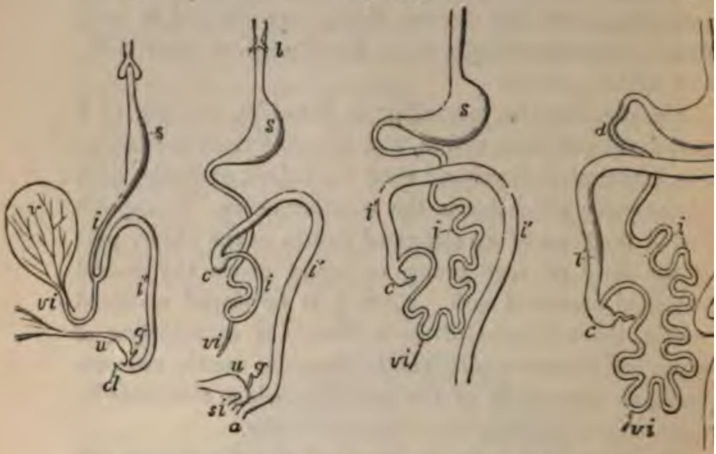
The Eustachian tube, the cavity of the tympanum, and the external auditory passage, are remains of the first branchial cleft. The membrana tympani divides the cavity of this cleft into an internal space, the tympanum, and the external meatus. The mucous membrane of the mouth, which is prolonged in the form of a diverticulum through the Eustachian tube into the tympanum, and the external cutaneous system, come into relation with each other at this point; the two membranes being separated only by the proper membrane of the tympanum.

Development of the Alimentary Canal.

The alimentary canal, the early stage of whose development has been already referred to (p. 746), is at first an

uniform straight tube, which gradually becomes divided into its special parts, stomach, small intestine, and large intestine (fig. 239). The stomach originally has the same direction as the rest of the canal; its cardiac extremity being superior, its pylorus inferior. The changes of position which the alimentary canal undergoes may be readily gathered from the accompanying figures.

A B *Fig.* 239.* C D



The principal glands in connection with the intestinal canal are the salivary, pancreas, and the liver. In Mammalia, each salivary gland first appears as a simple canal with bud-like processes (fig. 240), lying in a gelatinous nidus or blastema, and communicating with the cavity of

* Fig. 239. Outlines of the form and position of the alimentary canal in successive stages of its development (from Quain). A, alimentary canal, &c., in an embryo of four weeks; B, at six weeks; C, at eight weeks; D, at ten weeks; *l*, the primitive lungs connected with the pharynx; *s*, the stomach; *d*, duodenum; *i*, the small intestine; *i′*, the large; *c*, the cœcum and vermiform appendage; *r*, the rectum; *cl*, in A, the cloaca; *a*, in B, the anus distinct from *s i*, the sinus uro-genitalis; *v*, the yolk sac; *v i*, the vitello-intestinal duct; *u*, the urinary bladder and urachus leading to the allantois; *g*, genital ducts.

the mouth. As the development of the gland advances, the canal becomes more and more ramified, increasing at

Fig. 240.*

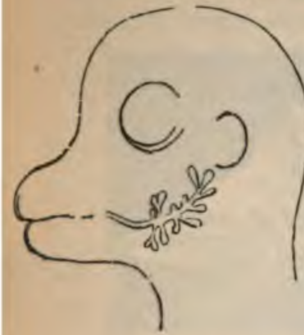


Fig. 241.†

the expense of the blastema in which it is still enclosed. The branches or salivary ducts constitute an independent system of closed tubes (fig. 241). The pancreas is developed exactly as the salivary glands.

The liver in the embryo of the bird is developed by the protrusion, as it were, of a part of the walls of the intestinal canal, in the form of two conical hollow branches which embrace the common venous stem (fig. 242). The outer part of these cones involves the omphalo-mesenteric vein, which breaks up in its interior into a plexus of capillaries, ending in venous trunks for the conveyance of the blood to the heart. The inner portion of the cones forms the cellular structure of the organ into which the

* Fig. 240. First appearance of the parotid gland in the embryo of a sheep.

† Fig. 241. Lobules of the parotid, with the salivary ducts, in the embryo of the sheep, at a more advanced stage.

blood-vessels extend, and in which they are, with the ducts, gradually developed. The gall-bladder is developed as a diverticulum from the hepatic duct.

Fig. 242.*

Development of the Respiratory Apparatus.

The lungs, at their first development, appear as small tubercles, or diverticula from the abdominal surface of the

Fig. 243.†

* Fig. 242. Rudiments of the liver on the intestine of a chick at the fifth day of incubation. 1, heart; 2, intestine; 3, diverticulum of the intestine on which the liver (4) is developed; 5, part of the mucous layer of the germinal membrane.

† Fig. 243, illustrates the development of the respiratory organs. A, is the œsophagus of a chick on the fourth day of incubation, with the rudiments of the trachea on the lung of the left side, viewed laterally: 1, the inferior wall of the œsophagus; 2, the upper wall of the same tube; 3, the rudimentary lung; 4, the stomach. B, is the same object seen from below, so that both lungs are visible. C, shows the tongue and respiratory organs of the embryo of a horse: 1, the tongue; 2, the larynx; 3, the trachea; 4, the lungs viewed from the upper side. After Rathke.

œsophagus. They are united at the anterior part of their circumference; and here a pedicle is formed which becomes elongated into the trachea (see fig. 243, A, B). Soon afterwards, the lung is seen to consist of a mass of cæcal tubes issuing from the branches of the trachea. (Fig. 243, C.) The diaphragm is early developed.

The Wolffian Bodies, Urinary Apparatus, and Sexual Organs.

The Wolffian bodies are organs peculiar to the embryonic state, and may be regarded as *temporary*, rather than *rudimental*, kidneys; for although they seem to discharge the functions of these latter organs, they are not developed into them. They probably bear the same relation to the persistent kidneys that the branchiæ of Amphibia do to the lungs which succeed them.

In Mammalia, the Wolffian bodies (fig. 244, W.) are bean-shaped, and are composed of transverse cæcal canals, united by an excretory duct (*w*) which leads from the lower extremity of the organ to the sinus urogenitalis of the fœtus (fig. 244, *ug*.) The kidneys (*r*) and supra-renal capsules (*sr*) are developed behind them. Their size is at first so great that they entirely conceal the kidneys; but in proportion as the latter bodies increase in size, they grow relatively smaller, and come to be placed more inferiorly. At length, towards the end of fœtal life, only an atrophied remnant of them is left. Their ducts, in the male, are ultimately developed to form the vas deferens and ejaculatory duct of each side; the vesiculæ seminales forming diverticula from their lower part. In the female, the ducts of the Wolffian bodies disappear.

The testicles or ovaries are formed independently at the internal excavated border of these organs; and at first it is not possible to say which of them—the testicle or ovary—the new formation is to become. Gradually, however, the special characters, belonging to one of

them are developed; and in either case the organ soon begins to assume a relatively lower position in the body; the ovaries being ultimately placed in the pelvis; while towards the end of fœtal existence the testicles descend into the scrotum, the testicle entering the internal inguinal ring in the seventh month of fœtal life, and completing its descent through the inguinal canal and external ring into the scrotum by the end of the eighth month. A pouch of peritoneum, the *processus vaginalis*, precedes it in its descent, and ultimately forms the tunica vaginalis or serous covering of the organ; the communication between the tunica vaginalis and the cavity of the peritoneum being closed only a short time before birth. In its descent, the testicle or ovary of course retains the blood-vessels, nerves, and lymphatics, which were supplied to it while in the lumbar region, and which are compelled to follow it, so to speak, as it assumes a lower position in the body. Hence the explanation of the otherwise strange fact of the origin of these parts at so considerable a distance from the organ to which they are distributed.

The means by which the descent of the testicles into the scrotum is effected are not fully and exactly known. It was formerly believed that a membranous and partly muscular cord, called the *gubernaculum testis*, which extends while the testicle is yet high in the abdomen, from its lower part, through the abdominal wall (in the situation of the inguinal canal) to the front of the pubes and lower part of the scrotum, was the agent by the contraction of which the descent was effected. It is now generally believed, however, that such is not the case; and that the descent of the testicle and ovary is rather the result of a general process of development in these and neighbouring parts, the tendency of which is to produce this change in the relative position of these organs. In other words, the descent is not the result of a mere mechanical action, by which the organ is dragged down to a lower

position, but rather one change out of many which attend the gradual development and re-arrangement of these organs. It may be repeated, however, that the details of the process by which the descent of the testicle into the scrotum is effected are not accurately known.

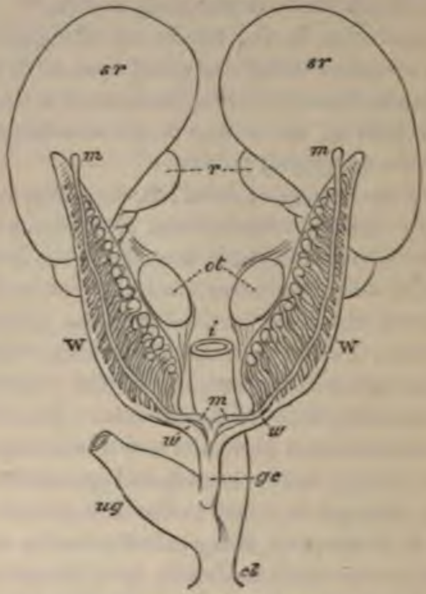
The homologue, in the female, of the gubernaculum testis, is a structure called the *round ligament of the uterus*, which extends through the inguinal canal, from the outer and upper part of the uterus to the subcutaneous tissue in front of the symphysis pubis.

At a very early stage of fœtal life, the efferent ducts of the Wolffian bodies of the kidneys and of the ovaries or testes, open into a receptacle formed by the lower end of the allantois, or rudimentary bladder; and as this communicates with the lower extremity of the intestine, there is for the time, a common receptacle or *cloaca* for all these parts, which opens to the exterior of the body through a part corresponding with the future anus. In a short time, however, the intestinal portion of the cloaca is cut off from that which belongs to the urinary and generative organs; a separate passage or canal to the exterior of the body, belonging to these parts, being called the *sinus urogenitalis*. Subsequently, this canal is divided, by a process of division extending from before backwards or from above downwards, into a 'pars urinaria' and a 'pars genitalis.' The former, continuous with the *urachus* (p. 749), is converted into the urinary bladder.

The Fallopian tubes, the uterus, and the vagina are developed from two threads of blastema, called the Müllerian ducts (fig. 244, *m*), which appear in front of the Wolffian bodies at about the time that these begin to change their relative position to neighbouring parts, and to decrease in size. The two Müllerian ducts are united below into a single cord, called the *genital cord*, and, from this are developed the vagina, as well as the cervix and the lower portion of the body of the uterus; while the

ununited portion of the duct on each side forms the upper part of the uterus, and the Fallopian tube. In certain cases of arrested or abnormal development, these portions

* *Fig.* 244.



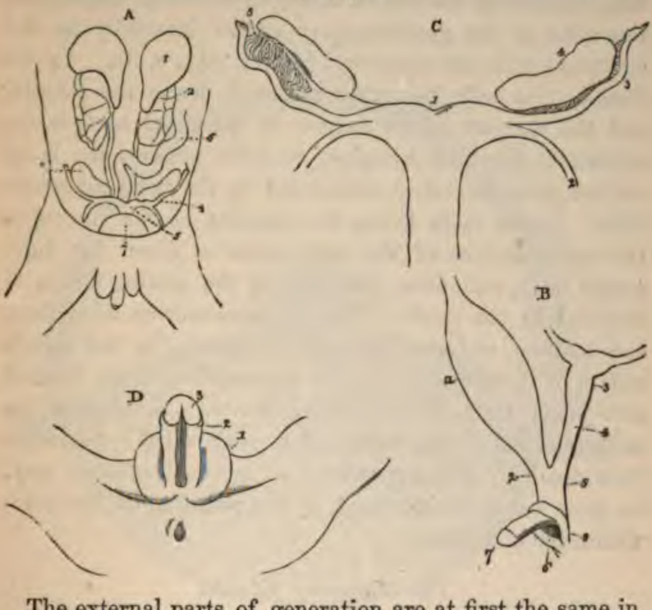
of the Müllerian ducts may not become fused together at their lower extremities, and there is left a cleft or horned condition of the upper part of the uterus, resembling a condition which is permanent in certain of the lower animals.

In the male, the Müllerian ducts have no special function, and are but slightly developed: the small prostatic pouch, or *sinus pocularis*, forms the atrophied remnant

* Fig. 244. Diagram of the Wolffian bodies, Müllerian ducts and adjacent parts previous to sexual distinction, as seen from before (from Quain). *sr*, the supra-renal bodies; *r*, the kidneys; *ot*, common blastema of ovaries or testicles; W, Wolffian bodies; *w*, Wolffian ducts; *m*, *m*, Müllerian ducts; *ge*, genital cord; *ug*, sinus urogenitalis; *i*, intestine; *cl*, cloaca.

of the genital cord, and is, of course, therefore, the homologue, in the male, of the vagina and uterus in the female.

Fig. 245.*



The external parts of generation are at first the same in both sexes. The opening of the genito-urinary apparatus

* Fig. 245. Urinary and generative organs of a human female embryo, measuring 3½ inches in length. A, general view of these parts; 1, supra-renal capsules; 2, kidneys; 3, ovary; 4, Fallopian tube; 5, uterus; 6, intestine; 7, the bladder. B, Bladder and generative organs of the same embryo viewed from the side; *a*, the urinary bladder (at the upper part is a portion of the urachus); 2, urethra; 3, uterus (with two cornua); 4, vagina; 5, part as yet common to the vagina and urethra; 6, common orifice of the urinary and generative organs; 7, the clitoris. C, Internal generative organs of the same embryo; 1, the uterus; 2, the round ligaments; 3, the Fallopian tubes (formed by the Müllerian ducts); 4, the ovaries; 5, the remains of the Wolffian bodies. D, external generative organs of the same embryo; 1, the labia majora; 2, the nymphæ; 3, the clitoris. After Müller.

is, in both sexes, bounded by two folds of skin, whilst in front of it there is formed a penis-like body surmounted by a glans, and cleft or furrowed along its under surface. The borders of the furrow diverge posteriorly, running at the sides of the genito-urinary orifice internally to the cutaneous folds just mentioned (see fig. 245, B, D). In the female, this body becoming retracted, forms the clitoris, and the margins of the furrow on its under surface are converted into the nymphæ, or labia minora, the labia majora pudendæ being constituted by the great cutaneous folds. In the male fœtus, the margins of the furrow at the under surface of the penis unite at about the fourteenth week, and form that part of the urethra which is included in the penis. The large cutaneous folds form the scrotum, and at a later period, namely, in the eighth month of development, receive the testicles, which descend into them from the abdominal cavity. Sometimes the urethra is not closed, and the deformity called hypospadias then results. The appearance of hermaphroditism may, in these cases, be increased by the retention of the testes within the abdomen.

The Mammary Glands.

The mammary glands, which may be considered as organs superadded to the reproductive system in man and other members of the class (Mammalia) which derives its name from them, are, in the essential details of their structure, very similar to other compound glands, as the pancreas and salivary glands; that is to say, they are composed of larger divisions or lobes, and these are again divisible into lobules,—the lobules being composed of the follicular extremities of ducts, lined by glandular epithelium. The lobes and lobules are bound together by areolar tissue; while, penetrating between the lobes, and covering the general surface of the gland, with the exception of the nipple, is a considerable quantity

of yellow fat, itself lobulated by sheaths and processes of tough areolar tissue (fig. 246) connected both with the skin in front and the gland behind; the same bond of connection extending also from the under surface of the gland to

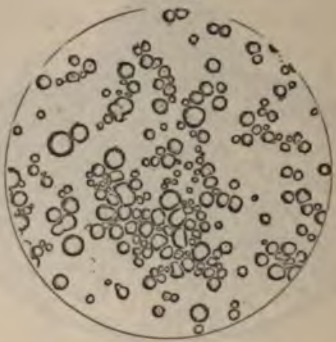
Fig. 246.*

the sheathing connective tissue of the great pectoral muscle on which it lies. The main ducts of the gland, fifteen to

* Fig. 246. Dissection of the lower half of the female mamma during the period of lactation (from Luschka). $\frac{2}{3}$.—In the left-hand side of the dissected part the glandular lobes are exposed and partially unravelled; and on the right-hand side, the glandular substance has been removed to show the reticular loculi of the connective tissue in which the glandular lobules are placed: 1, upper part of the mamilla or nipple; 2, areola; 3, subcutaneous masses of fat; 4, reticular loculi of the connective tissue which support the glandular substance and contain the fatty masses; 5, one of three lactiferous ducts shown passing towards the mamilla where they open; 6, one of the sinus lactei or reservoirs; 7, some of the glandular lobules which have been unravelled; 7′, others massed together.

twenty in number, called the *lactiferous* or *galactophorous* ducts, are formed by the union of the smaller ducts, and open by small separate orifices through the nipple. Just before they enter the base of the nipple, these ducts are dilated (6, fig. 246); and, during lactation, the period of active secretion by the gland, they form reservoirs for the milk, which collects in them and distends them. The walls of the gland-ducts are formed of areolar and elastic tissue, and are lined internally by a fine mucous membrane, the surface of which is covered by squamous or spheroidal epithelium.

Fig. 247.*



The nipple, which contains the terminations of the lactiferous ducts, is composed also of areolar tissue, and contains unstriped muscular fibres. Blood-vessels are also freely supplied to it, so as to give it a species of erectile structure. On its surface are very sensitive papillæ; and around it is a small area or *areola* of pink or dark-tinted skin, on which are to be seen small projections formed by minute secreting glands.

Blood-vessels, nerves, and lymphatics are plentifully supplied to the mammary glands; the calibre of the blood-vessels, as well as the size of the glands, varying very

* Fig. 247. Globules and molecules of cow's milk $\frac{400}{1}$.

greatly under certain conditions, especially those of pregnancy and lactation.

The secretion of milk, which under ordinary healthy circumstances only occurs after parturition, if we except the slight secretion which takes place in the latter months of pregnancy, is effected by the epithelial cells lining the ultimate follicles of the mammary gland. The process does not differ from secretion in glands generally (see p. 404), and need not here be particularly described.

Under the microscope, milk is found to contain a number of globules of various size (fig. 247), the majority about $\frac{1}{10000}$ of an inch in diameter. They are composed of oily matter, probably coated by a fine layer of albuminous material, and are called *milk-globules*; while, accompanying these, are numerous minute particles, both oily and albuminous, which exhibit ordinary molecular movements. The milk, which is secreted in the first few days after parturition, and which is called the *colostrum*, differs from ordinary milk in containing a larger quantity of solid matter; and under the microscope are to be seen certain granular masses called *colostrum-corpuscles*. These, which appear to be small masses of albuminous and oily matter, are probably secreting cells of the gland, either in a state of fatty degeneration, or, as Dr. Gedge remarks, old cells which in their attempts at secretion under the new circumstances of active need of milk, are filled with oily matter; which, however, being unable to discharge, they are themselves shed bodily to make room for their successors.

The specific gravity of human milk is about 1030. Its chemical composition has been already mentioned (p. 246).

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